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Key Points:

- The alpine meadow was a strong methane sink on the Qinghai-Tibetan Plateau
- Obvious diurnal and seasonal dynamics of net CH₄ flux were observed
- The key controlling factors for the temporal dynamics varied with scales

Supporting Information:

- Supporting Information S1
- Table S1
- Table S2
- Data Set S1
- Data Set S2

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Diel and Seasonal Dynamics of Ecosystem-Scale Methane Flux and Their Determinants in an Alpine Meadow

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Abstract Temporal variations of methane flux (FCH₄) and its underlying mechanisms still remain poorly understood. To quantify diurnal and seasonal patterns of FCH₄ and investigate its determinants, we monitored FCH₄ using eddy covariance in an alpine meadow on the Qinghai-Tibetan Plateau, China, from June 2015 to December 2016. As a strong CH₄ sink, the alpine meadow on the Qinghai-Tibetan Plateau consumed 0.41 ± 0.04 Tg CH₄/year. There was an obvious diurnal pattern with more CH₄ uptakes during the nighttime than the daytime for both growing and nongrowing season. The diurnal FCH₄ during the growing and nongrowing season were positively correlated with air temperature (Ta), volumetric water content, friction velocity (u^*), and vapor pressure deficit. The growing season FCH₄ showed a significant quadratic polynomial relationship with the canopy conductance (G_w) and gross primary production. FCH₄ was significantly higher in the growing season than in the nongrowing season. The seasonal FCH₄ was negatively correlated with soil temperature and net radiation (Rn) but not with volumetric water content and gross primary production. Ridge regression models indicated that Ta and u^* explained 83% of the variation in the diel dynamics of FCH₄ during the growing season and explained 72% of the variation during the nongrowing season. Rn accounted for 49% of variations of FCH₄ at the seasonal scale. The temporal patterns and the environmental controlling factors revealed in this study may improve model parameterization for biosphere-atmosphere CH₄ exchange simulation as well as the methane budget estimation.

Plain Language Summary Methane (CH₄) is a very important greenhouse gas, responsible for about 20% of the warming induced by long-lived greenhouse gases since 1750, and its impact is second only after carbon dioxide (CO₂). However, we know much less about CH₄ compared to CO₂. Many basic but important questions about CH₄ still remain unanswered, such as the diurnal and seasonal patterns of CH₄ flux as well as the controlling factors of these temporal dynamics of CH₄ flux. To answer these questions, we monitored the CH₄ flux continuously in an alpine meadow ecosystem located on the eastern Qinghai-Tibetan Plateau, China, from June 2015 to December 2016. At the diurnal scale, we found that the CH₄ uptake at nighttime was higher than at daytime. At the seasonal scale, we found higher CH₄ uptake during summer than winter. We also found that CH₄ fluxes were determined by air temperature and net radiation at the diurnal scale and seasonal scale, respectively. The temporal patterns and the controlling factors revealed in this study may help to improve the prediction of CH₄ exchange processes and the estimation of methane budget from the regional to the global scale.

1. Introduction

Methane (CH₄)-induced radiative forcing is 0.97 (0.74 – 1.2) W/m² since 1750, responsible for about 20% of the warming caused by long-lived greenhouse gases, second only to carbon dioxide (Herbst et al., 2011; Kirschke et al., 2013; Schulze et al., 2009; Shindell et al., 2009). CH₄ has a long lifetime of about 12 years and a high Global Warming Potential 28 times as large as that of carbon dioxide (CO₂; Intergovernmental Panel on Climate Change, 2013). The concentration of atmospheric CH₄ has consistently increased from 700 to over 1,819 ppb since the era of industrialization to 2012 (Wei et al., 2015). The sources and sinks of CH₄ have attracted widespread attention (Heimann, 2011;

Nisbet et al., 2014; Van Amstel, 2012). Natural aerobic soils are the second largest CH₄ sink only after reaction with OH in the troposphere, accounting for about 10% of the global CH₄ sink (Curry, 2007; Dutaur & Verchot, 2007; Lowe, 2006). However, there remains wide variations and large uncertainties with respect to the magnitude of the CH₄ consumed by global soils during the 2000s in different studies, ranging from 22.6 to 30 Tg CH₄/year based on bottom-up approaches (Curry, 2007; Kirschke et al., 2013; Lowe, 2006; Spahni et al., 2011; Tian et al., 2016). The large uncertainty in global soil CH₄ consumption is mainly due to sparse observation sites and lack of knowledge of the controlling mechanism of CH₄ variation of different ecosystems. So it is important to study the temporal pattern of the CH₄ sink and the controlling factors in order to achieve a more accurate and precise estimation of the global methane budget.

CH₄ flux is the balance between the consumption by methanotrophic microbes and the production by methanogenic microbes and the transport between the atmosphere and the surface. Therefore, biotic and abiotic factors that control these processes may also affect CH₄ flux. Hence, temporal dynamics in net methane fluxes is expected to couple with the temporal dynamics of controlling processes (Long et al., 2010). The diurnal variations of methane emissions have been reported in wetland ecosystems. Some studies showed one-peak diurnal pattern or two-peak diurnal pattern (Ge et al., 2018; Kim et al., 1998; Koch et al., 2007; Kowalska et al., 2013; Long et al., 2010; Song et al., 2015; Suyker et al., 1996; Whiting & Chanton, 1996), while others exhibited no clear diurnal variation patterns (Herbst et al., 2011; Hommeltenberg et al., 2014; Kormann & Meixner, 2001; Rinne et al., 2007). Diurnal patterns of methane flux were generally affected by solar radiation, soil temperature, plant community, and plant morphological and physiological characteristics (Long et al., 2010). Vascular plants, especially, were able to influence the production, oxidation, and transport of CH₄, through modulating rhizosphere exudation, specialized aerenchyma tissue, or stomatal conductance, all of which had a strong effect on the diurnal variation of CH₄ flux (Chu et al., 2014; Garnet et al., 2005; Long et al., 2010). The net CH₄ fluxes (uptake or emission) of many different ecosystems showed an obvious seasonal pattern, which is significantly higher during the growing season than that during the nongrowing season (Guo et al., 2016; Hargreaves et al., 2001; He et al., 2014; Herbst et al., 2011; Hommeltenberg et al., 2014; Long et al., 2010; Rinne et al., 2007; Wang et al., 2000; Wilson et al., 2009). However, the diurnal and seasonal dynamics of net methane uptake and its controlling factors in grassland, especially the alpine grassland, were rarely investigated (Qi et al., 2002; Wang et al., 2003; Zhang et al., 2004).

Known as the third pole of the world with an average elevation about 4,000 m, Qinghai-Tibetan Plateau is very sensitive to the global climate change (Liu & Chen, 2000; Yao & Zhu, 2006; Zhang et al., 2015). Alpine meadow is one of the most important ecosystems on the Qinghai-Tibet Plateau, covering an area of $\sim 70 \times 10^4$ km² and accounting for $\sim 35\%$ of the total plateau (Cao et al., 2008; Ni, 2002; Zhang & Liu, 2003; Zheng et al., 2012). The alpine meadow of Qinghai-Tibetan Plateau is generally the sink of the atmospheric CH₄, with a mean methane absorption rate about 31.29 ± 21.78 mg CH₄·m⁻²·hr⁻¹ (Kato et al., 2013; Wang et al., 2014). Qinghai-Tibetan Plateau grassland ecosystem is dominated by alpine meadow, which is ranked the first largest methane uptake of grasslands in China. It consumed about 0.284 Tg CH₄/year, $\sim 44\%$ of the total CH₄ uptake of grasslands in China (Wang et al., 2014). Some studies have shown that soil methane uptake of alpine meadow tended to increase under the joint impacts of climate change and anthropogenic activities (Chen et al., 2013a, 2013b; Zheng et al., 2012). However, the temporal patterns and its controlling factors of the CH₄ flux of alpine meadow remain unclear because almost all of the previous studies were conducted in chambers with only few discontinuous measurements during the growing season. It is impossible to monitor the diurnal and seasonal dynamics, especially in the nongrowing season. The mechanisms underlying the temporal dynamics of CH₄ fluxes are far from clear.

The eddy covariance technique provides integrated continuous measurements over a large area and may increase our understanding of the temporal dynamics and the controlling factors of CH₄ emissions. In this study, we continuously monitored the CH₄ flux of an alpine meadow ecosystem located on the eastern Qinghai-Tibetan Plateau with half hour resolution based on the eddy covariance technique for two growing seasons. The main objectives are (1) revealing diurnal and seasonal patterns of the methane flux in an alpine meadow, (2) investigating key factors controlling the diurnal and seasonal variation of the methane flux, and (3) quantifying the role of alpine meadows across the plateau in consuming methane.

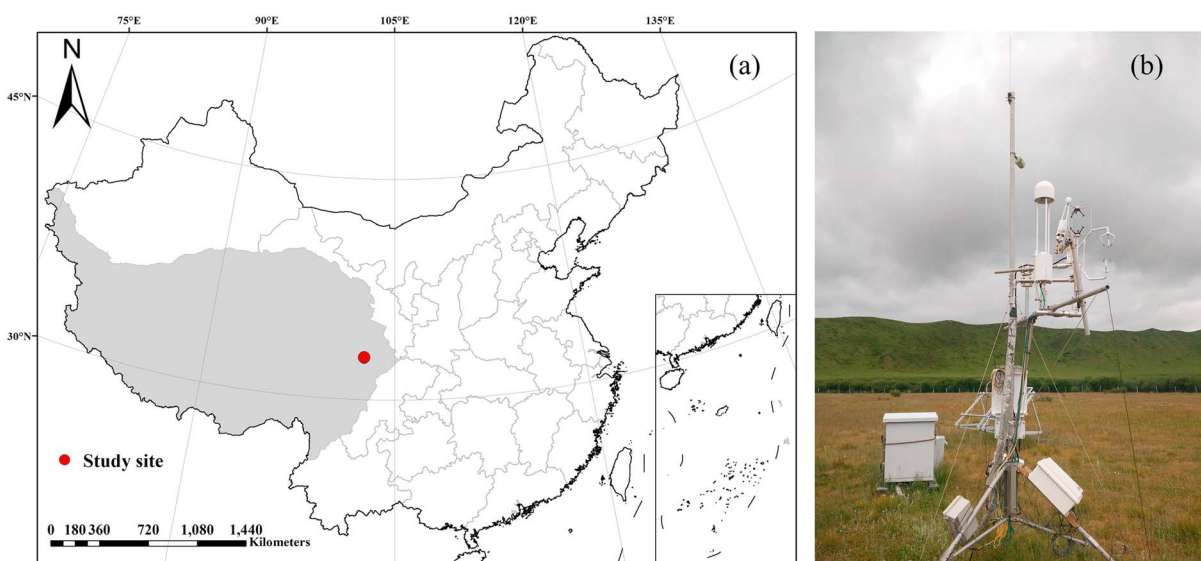


Figure 1. (a) Study site on the Tibetan Plateau. (b) The eddy covariance measurements at our study site.

2. Materials and Methods

2.1. Site Description

The methane flux was measured at an alpine meadow in the Qinghai-Tibetan Plateau Research Center of Southwest Minzu University (32°48'N and 102°33'E; 3,500 m a.s.l.), located in Hongyuan County, Sichuan Province, China, on the Eastern edge of the Qinghai-Tibetan Plateau (Figure 1a). The Hongyuan alpine meadow has a continental plateau monsoon climate which is characterized by strong solar radiation (the annual total solar radiation is about 6,194 MJ/m²) with long, cold winters and short, cool summers. The annual mean temperature of this region is ~1.5 °C (based on the routine meteorology data from 1961 to 2013). July is the warmest month with a mean monthly temperature of 11.1 °C, while January is the coldest month with a mean monthly temperature of -9.7 °C. The annual mean precipitation is 747 mm (1961–2013), and more than 80% of the precipitation is concentrated in the growing season from May to September.

The vegetation in this alpine meadow is dominated by *Deschampsia caespitosa*, *Poa Pratensis*, *Elymus nutans*, *Agrostis hugoniana*, *Kobresia setchwanensis*, *Oxytropis kansuensis*, *Vicia sepium*, *Anemone rivularis*, *Potentilla anserine*, *Polygonum viviparum*, and *Ligularia virgaurea*. The soil in the region is classified as Mat Cry-gelic Cambisol according to the Chinese classification (Song et al., 2017). The soil thickness is 0.3–0.5 m, and the surface soil bulk density (0–20 cm) is 0.89 ± 0.04 g/cm³. The soil pH value is 6.24 ± 0.09 . Top soil (0–10 cm) organic carbon (C) is 37.36 ± 0.51 g/kg, and the total nitrogen (N) is 3.51 ± 0.04 g/kg.

2.2. Eddy Covariance Measurements and Meteorological Measurements

An open-path eddy covariance measurement system was installed at a height of 2 m above the alpine meadow from 1 June 2015 to 31 December 2016 (Figure 1b). The eddy covariance system consists of a three-dimensional sonic anemometer (CSAT3; Campbell Scientific Inc. (CSI), Logan, USA), an open-path CO₂/H₂O infrared gas analyzer (LI-7500A; Li-COR Inc, Lincoln, NE, USA), and an open-path CH₄ infrared gas analyzer (LI-7700; Li-COR). Data are logged at 10 Hz with a datalogger (CR5000, Campbell Scientific, Utah, USA).

Meteorological data were measured simultaneously with the eddy covariance system. Air temperature (Ta) and relative humidity were measured using HMP45C temperature probe (VAISALA, Finland). Soil volumetric water content (VWC) and soil temperature (T_{soil}) were measured at a depth of 5, 10, 20, 40, and 80 cm using CS655 probe (CSI). Precipitation (mm) was measured with a tipping bucket rain gauge (TE525, CSI), and net radiation (Rn) was measured with a four-component radiometer (CNR4, Kipp and Zonen, Delft, Netherlands). Meteorological data are logged half-hourly with a datalogger (CR1000, Campbell Scientific, Utah, USA).

2.3. Data Processing and Analysis

We preprocessed raw data (.ghg) using EddyPro 6.2.0 software. In this software, methane flux (F_{CH_4}) were computed in terms of the covariance between vertical wind velocity (w) and mixing ratio (χ_c) fluctuations, times the density in dry air (ρ) with averaging time set as 30 min

$$F_{CH_4} = \rho \overline{w' \chi'_c} \quad (1)$$

where “—” represents time average and “'” represents the fluctuation, that is, the deviation between the instantaneous value and the mean value.

The Eddypro software applied processing as follows: double axis rotation, block averaging, maximum covariance with default, fully configurable statistical tests (including spike count/removal, amplitude resolution, dropouts, absolute limits, skewness, and kurtosis), Webb-Pearman-Leuning density fluctuations (WPL correction), sonic virtual temperature correction, spectral correction, the incorporated frequency response correction, angle of attack correction, quality check-flagging, and spectroscopic corrections for LI7700. We applied an approximate analytical footprint model (Hsieh et al., 2000) to estimate the contributing source areas to scalar flux measurement. Under unstable atmospheric conditions, the observed fluxes were mainly contributed by the nearby area within 250 m (Figure S1a in the supporting information), while under stable atmospheric conditions, the flux contributing source of our eddy covariance flux tower could be as far as about 4,000 m. The footprint model showed that peak distance from measuring point to the maximum contributing source area was 8.8 m (Figures S1c and S1d), and the Fetch to Height ratio was 90:1. After preprocessing of EddyPro, methane fluxes were converted from 10 Hz to half hour interval and the data coverage was 58%. First, we filtered the data beyond the range of -0.1 to $0.005 \mu\text{mol}/\text{m}^2/\text{s}$ based on empirical value and 38% of the data was left in the database. Second, because precipitation may disturb the atmosphere flow and interfere with the observation, we removed the data during the rainfall event and 37% of the data was left in the database. Finally, to avoid errors due to CH_4 storage during calm conditions, we removed the data when the friction velocity (u^*) was less than 0.1 m/s at nighttime. After this final step, 34% of the data were kept in the database. Days with data coverage larger than 30% were considered as valid days and used for further calculation and analysis. We investigated the diurnal cycle by averaging every half hour flux data across all valid days and created a representative day with 48 data points. For the monthly average, to avoid the bias caused by the unbalanced data points in different days, we first calculated a representative day for that month by averaging every half hour flux data across valid days during the month. Then the monthly average was calculated by averaging the half hour flux data of the representative day. A detailed description of the data coverage in each time of the day and year is provided in Tables S1 and S2. The positive value means CH_4 emission from soil to atmosphere, while the negative value means CH_4 uptake from atmosphere to the underlying surface.

CH_4 flux data were divided into two time periods according to physical conditions and plant growth: (a) a growing season, ranging from 21 April to 31 October and (b) a nongrowing season, ranging from 1 November to 20 April of the next year.

Gross primary productivity (GPP) was partitioned from CO_2 flux data (NEE, net ecosystem exchange) of the same eddy covariance measurement system as CH_4 flux. First, missing data of daytime NEE during the growing season were gap filled by a rectangular hyperbolic regression as follows (Falge et al., 2001).

$$NEE_{\text{daytime}} = -\frac{\alpha F_{\text{max}} \text{PPFD}}{\alpha \text{PPFD} + F_{\text{max}}} + R_{\text{eco}} \quad (2)$$

where NEE_{daytime} ($\mu\text{mol}/\text{m}^2/\text{s}$) is NEE at daytime, α is the apparent quantum yield, F_{max} ($\mu\text{mol}/\text{m}^2/\text{s}$) is the maximum CO_2 flux at infinite light, PPFD ($\mu\text{mol}/\text{m}^2/\text{s}$) is photosynthetic photon flux density, and R_{eco} ($\mu\text{mol}/\text{m}^2/\text{s}$) is the ecosystem respiration.

Second, nighttime missing NEE data were gap filled by using an exponential equation against the air temperature (Lloyd & Taylor, 1994).

$$NEE_{\text{nighttime}} = a \exp(bT_{\text{air}}) \quad (3)$$

where $NEE_{\text{nighttime}}$ is nighttime NEE, that is, the ecosystem respiration (R_{eco}) and a and b are two empirical coefficients. Daytime ecosystem respiration can be estimated by expanding this equation to daytime.

Table 1

Ridge Regression Model at Diurnal Scale During the Nongrowing Season and the Growing Season and at Seasonal Scale, Their Equation, Adj. R^2 (Adjusted R^2), and Significance

Period	Equation model	Adj. R^2	Significance
Diurnal scale during the nongrowing season	$FCH4 = 0.009 \cdot u^* + 0.009 \cdot Ta$	0.72	***
Diurnal scale during the growing season	$FCH4 = 0.015 \cdot Ta + 0.016 \cdot u^*$	0.83	***
Seasonal scale	$FCH4 = (-4.300E-03) \cdot Rn$	0.49	**

Note. FCH4 = net methane flux; u^* = friction velocity; Ta = air temperature; Rn = net radiation. Coefficients of these equation models were standardized.

** $P < 0.05$. *** $P < 0.001$.

Finally, GPP can be calculated as

$$GPR_{eco} - NEE \quad (4)$$

where R_{eco} is the daytime ecosystem respiration, NEE is the daytime net ecosystem exchange of carbon.

The canopy conductance for water vapor (G_w , mm/s) was calculated by inverting the Penman-Monteith equation (Xu et al., 2018):

$$\frac{1}{G_w} = \frac{r_a}{\gamma} \left(\frac{\Delta Rn + \rho C_p VPD / r_a}{\lambda ET} - \Delta - \gamma \right) \quad (5)$$

where r_a is the inverse of aerodynamic conductance (s/mm), γ is the psychrometric constant (kPa/K), VPD is the saturation water vapor pressure deficit (kPa), Δ is the slope of the VPD curve with temperature (kPa/K), Rn is the net radiation, ρ is the air density (kg/m^3), C_p is the specific heat capacity of air (J/kg/K), and λET is the latent heat (LE) measured by the eddy covariance (W/m^2).

r_a is the inverse of aerodynamic conductance; it is calculated as

$$r_a = \frac{\ln[(z-d)/z_0]}{k^2 u^*} \quad (6)$$

where z_0 is the surface roughness (0.1 hr), h is the mean canopy height (0.2 m), z is the measurement height (2 m), d is the zero plane displacement (0.65 hr), k is the von Kármán constant, and u^* is the friction velocity at height z .

We used three regression analyses to investigate key factors controlling the diurnal and seasonal variation of the methane flux. First, we used bivariate regression to explore the relationship between methane flux and each environmental or biotic factor, respectively, including Ta, Rn, T_{soil} at the depth of 10 cm and VWC at the depth of 5 cm, u^* , VPD, G_w , GPP on different time scales. Second, partial regression statistics were used to evaluate the relationship (slope and variance) between net methane flux and each covariate while controlling for the influence of all other independent model covariates. Third, to solve the collinearity problem and determine the relative importance of each influencing factor while explaining correlated variation among all variables, we used ridge regression for different time scales. Considering the large spatial heterogeneity of soil moisture and the little representativeness and accuracy of its diurnal dynamics, VWC was excluded for the ridge regression at diurnal scale during the growing season and the nongrowing season.

In addition, we performed time lag analysis for net methane flux and GPP on the diurnal scale in the growing season.

Based on the above analysis, we further estimated the total annual CH_4 uptake of alpine meadows on the Qinghai-Tibetan Plateau by upscaling our seasonal regression equation to the same ecosystem in the whole region. Since only net radiation (Rn) entered the regression model at the seasonal scale (Table 1), we applied zonal statistics to Rn raster data set and the corresponding map of vegetation type on the Qinghai-Tibetan Plateau to calculate the mean Rn of the alpine meadows. Substituting this mean value into the seasonal equation the total CH_4 consumption by alpine meadows on the Qinghai-Tibetan Plateau can be obtained. Net radiation (Rn) data were from the National Earth System Science Data Sharing Infrastructure,

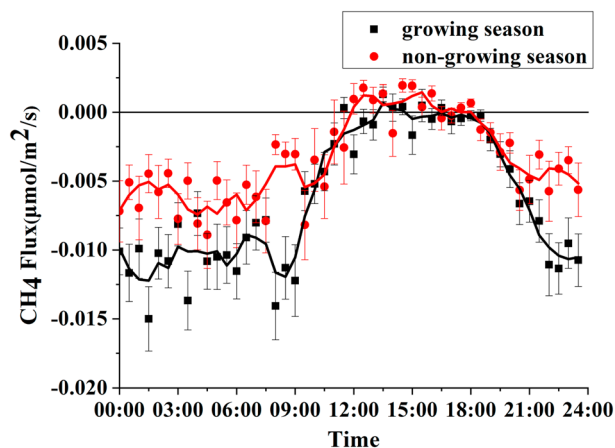


Figure 2. Diurnal patterns of net methane flux during the nongrowing season and the growing season. The black line represents the moving average of 3 hr during the growing season; the red line represents the moving-average of 3 hr during the nongrowing season. Vertical bars represent the standard error of the mean.

National Science & Technology Infrastructure of China (<http://www.geo-data.cn>). The raster data were the mean annual value of the surface net radiation data in the 2000s and spatially interpolated from 127 meteorology stations on the Qinghai-Tibetan Plateau. The spatial resolution of both the Rn data set and the vegetation type map is 1 km × 1 km.

3. Results

3.1. Diurnal Dynamics

CH₄ flux showed similar diurnal dynamics in the growing season and nongrowing season (Figure 2). The diurnal CH₄ flux pattern of the growing season was characterized by a strong uptake during the nighttime and a weak uptake during the daytime. The mean diurnal uptake rate of CH₄ flux fluctuated around $-0.0125 \mu\text{mol}/\text{m}^2/\text{s}$ between 0:00 and 9:00, then gradually declined until 11:00, fluctuated around $0 \mu\text{mol}/\text{m}^2/\text{s}$ between 11:00 and 18:00, and increased again after 18:00. Compared with the growing season, the diurnal variation of the CH₄ flux in the nongrowing season was relatively small. The alpine meadow was a methane sink between 0:00 and 9:00 and 18:00–24:00 and a nearly methane neutral between 11:00 and 18:00.

3.2. Seasonal Dynamics

The CH₄ flux showed a seasonal dynamic with a significantly higher net uptake during the growing season (May–October) than the nongrowing season (November–April; Figure 3). The highest uptake rate of CH₄ flux occurred in the peak growing stage (July and August) in 2015 and 2016, with a value of $-927.5 \mu\text{mol}/\text{m}^2/\text{day}$ in July of 2015 and $-703.9 \mu\text{mol}/\text{m}^2/\text{day}$ in August of 2016. There was a gap from November 2015 to January 2016 due to instrument malfunction, so the CH₄ flux variation of these 3 months was not clear.

3.3. Controlling Factors for the Diurnal and Seasonal Dynamics

At the diurnal scale in the nongrowing season, the net CH₄ flux significantly increased with the air temperature (T_a ; $p < 0.001$), VWC at 5 cm (VWC at 5 cm; $p < 0.01$), friction velocity (u^* ; $p < 0.001$), and vapor pressure deficit (VPD; $p < 0.001$; Figures 4a–4d). During the growing season, there were significant positive linear correlation relationships between the net CH₄ flux and T_a ($p < 0.001$), VWC at 5 cm ($p < 0.001$), u^* ($p < 0.001$), and VPD ($p < 0.001$; Figures 5a–5d). CH₄ flux and the canopy conductance for water vapor (G_w) had a significant quadratic polynomial relationship ($p < 0.001$) with stronger CH₄ uptake under both low and high canopy conductance (Figure 5e). There was a significant quadratic polynomial relationship between net CH₄ flux and GPP with a lag time of 1.5 hr ($p < 0.001$; Figure 5f). Partial regression found no significant relationship between net CH₄ flux and climate factors during the nongrowing season (Figures S2a–S2d), indicating collinearity among these climate variables. For the growing season, partial regression showed that the net CH₄ flux increased with T_a ($p = 0.01$), VWC at 5 cm ($p < 0.001$) and VPD ($p = 0.01$; Figures S3aa, S3b, and S3d). Net methane flux decreased with u^* ($p = 0.01$; Figure S3c) while G_w and GPP had no independent influence on the variation of net CH₄ flux (Figures S3e and S3e f).

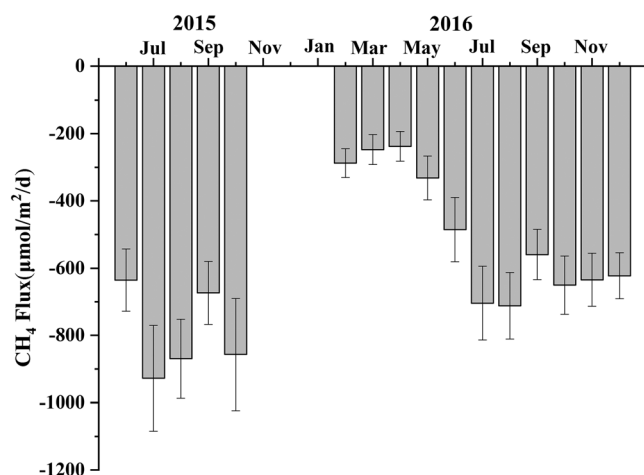


Figure 3. Seasonal dynamic of net methane flux from June 2015 to December 2016. Vertical bars represent the standard error of the mean.

At the seasonal scale, CH₄ flux was negatively correlated with soil temperature at 10 cm (T_{soil} at 10 cm; $p < 0.05$; Figure 6a) and net radiation (Rn; $p < 0.01$; Figure 6c) and CH₄ uptake was greater when T_{soil} and Rn were higher, but VWC at 5 cm did not affect CH₄ flux (Figure 6b). There was no significant relationship between the net CH₄ flux and GPP (Figure 6d). When the influences of all other influencing

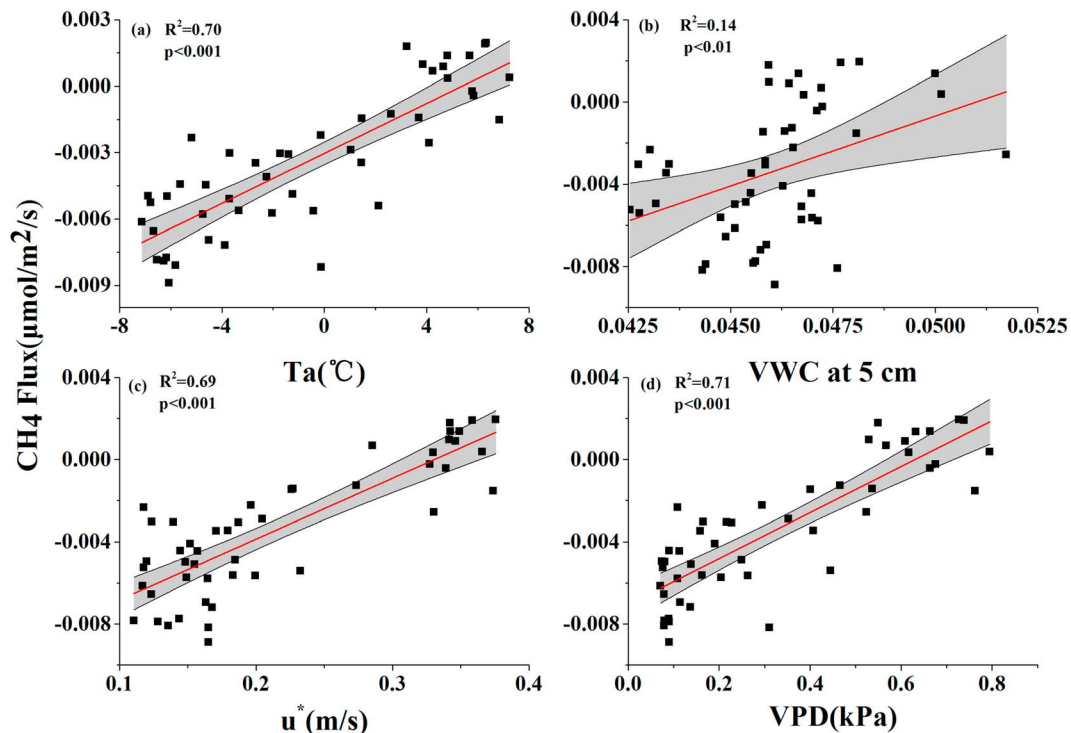


Figure 4. Relationship between net methane flux (CH_4 Flux) and (a) air temperature (T_a), (b) volumetric water content at the depth of 5 cm (VWC at 5 cm), (c) u^* (Friction velocity), and (d) vapor pressure deficit (VPD) at diurnal scale during nongrowing season. Shaded areas represent 95% confidence intervals.

variables were controlled, only R_n had a significant influence on the seasonal variation of net methane flux (Figure S4c; $p < 0.05$).

3.4. Predictors of Net Methane Flux and the Regional Estimation

We used ridge regression to establish the regression equations between net methane flux and influencing factors at different time scales (Table 1). T_a and u^* in combination explained 72% of the variation in CH_4 at the diurnal scale during the nongrowing season. For the diurnal dynamics in the growing season, T_a and u^* were also the main predictors and explained 83% variation of CH_4 . R_n was the only factor included in the seasonal model and accounted for 49% of the variation in CH_4 .

We then used those equations to estimate the annual CH_4 uptake by alpine meadow on the Qinghai-Tibetan Plateau. The estimated CH_4 uptake ranged from 0.33 to 0.81 $\text{g CH}_4 \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Figure 7). The CH_4 sink strength in the Southwest area was higher than that in the Northeast area of alpine meadow. The total annual CH_4 consumption by the whole alpine meadow on the Qinghai-Tibetan Plateau was estimated to be $0.41 \pm 0.04 \text{ Tg CH}_4/\text{year}$.

4. Discussion

4.1. Diurnal Dynamics and Their Controls

Previous studies have conflicting results on the diurnal dynamics of CH_4 flux, which was detected in some ecosystems (Dong et al., 2000; Qi et al., 2002; Wang et al., 2003; Zhang et al., 2004) but not in others (Imer et al., 2013; MalJanen et al., 2002; Steinkamp et al., 2001). We observed a very clear diurnal dynamic in methane flux during both growing and nongrowing seasons in an alpine meadow. Based on discontinuous measurements, some previous studies also found diurnal variations in grassland and forest ecosystems. Some of the reports agreed with our study with a strong uptake during nighttime and a weak uptake during daytime (Dong et al., 2000; Qi et al., 2002; Wang et al., 2003; Zhang et al., 2004), while others reported opposite patterns with a weak uptake during nighttime and a strong uptake during daytime (Qi et al., 2004). All of these previous reports did not explore mechanisms contributing to the diurnal pattern. In this study, changes in temperature and soil moisture determined the diurnal CH_4 flux variations. Therefore, previous reports

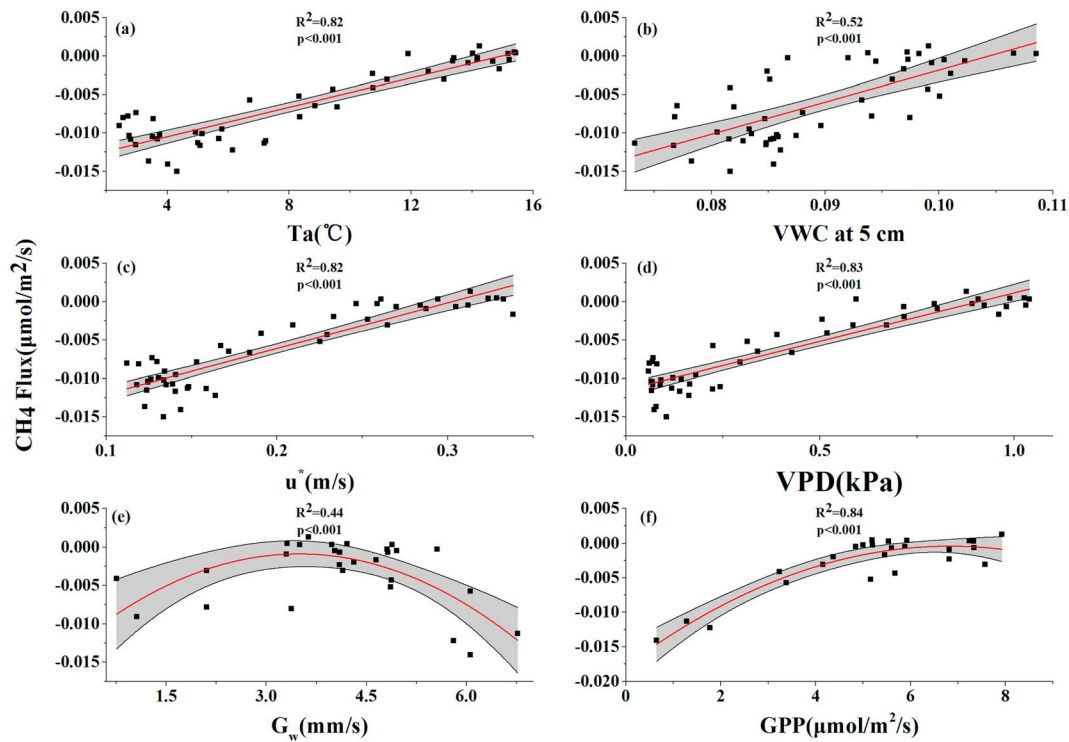


Figure 5. Relationship between net methane flux (CH_4 Flux) and (a) air temperature (T_a); (b) volumetric water content at the depth of 5 cm (VWC at 5 cm); (c) Friction velocity (u^*); (d) Vapor pressure deficit (VPD); (e) Canopy conductance (G_w); (f) gross primary productivity (GPP) at diurnal scale during growing season. Shaded areas represent 95% confidence intervals.

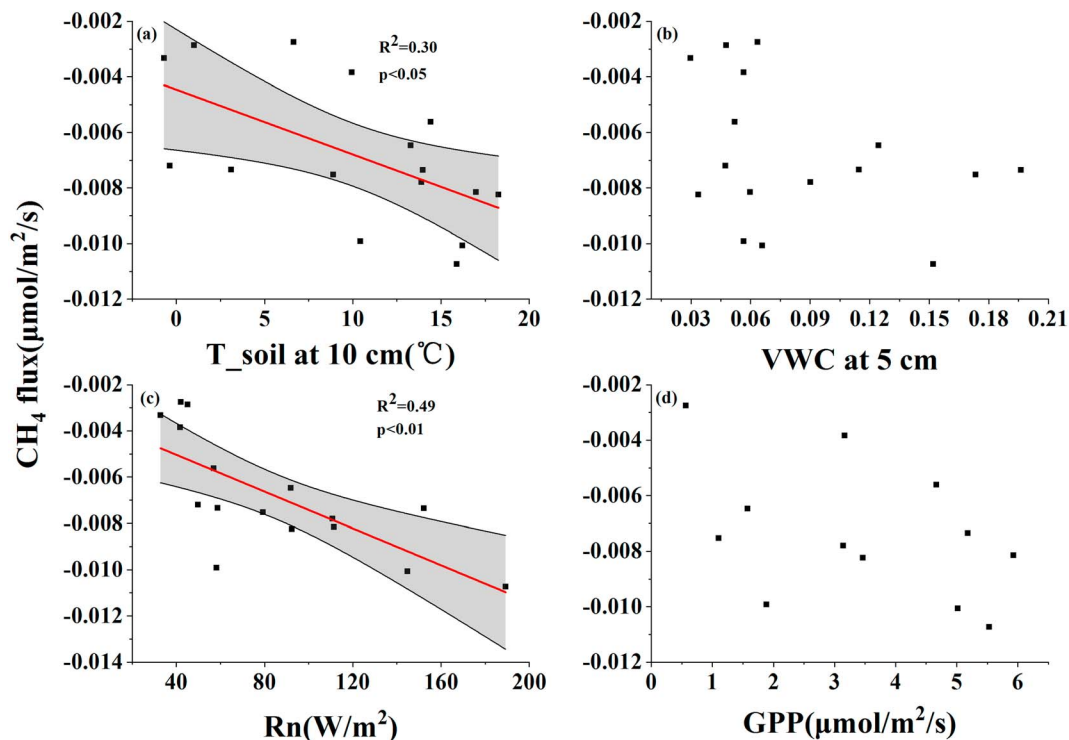


Figure 6. Relationship between net methane flux (CH_4) and (a) soil temperature at the depth of 10 cm ($T_{\text{soil at 10 cm}}$), (b) volumetric water content at the depth of 5 cm (VWC at 5 cm), (c) net radiation (R_n), and (d) gross primary productivity (GPP) at seasonal scale. Shaded areas represent 95% confidence intervals.

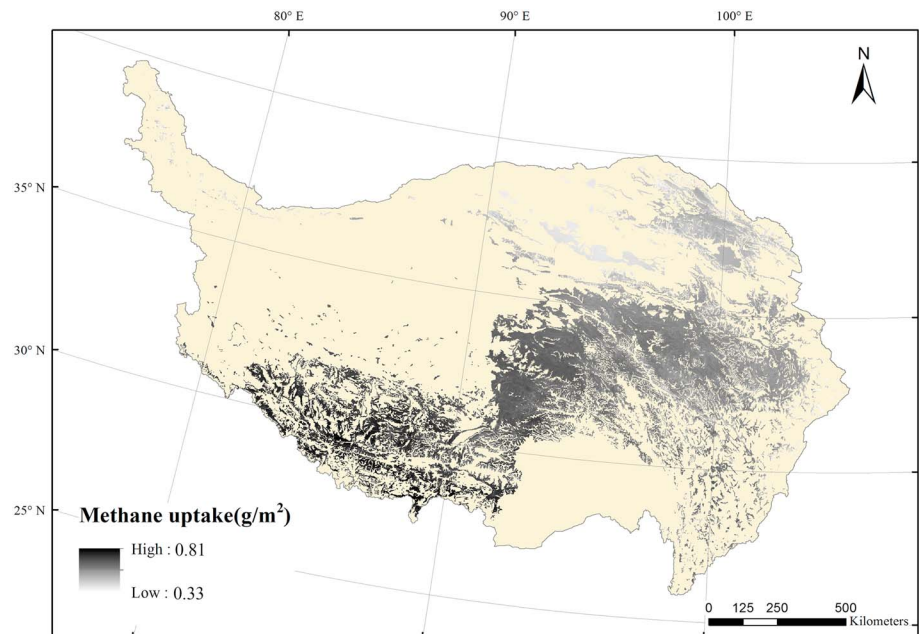


Figure 7. Spatial distribution of estimated annual CH₄ uptake (g CH₄ m²/year) by alpine meadow on the Qinghai-Tibetan Plateau.

that did not find the diurnal pattern of CH₄ flux can be partly explained by the fact that the amplitude of changes in daily temperature or soil moisture in the ecosystems they studied is too small to cause obvious dynamics in net CH₄ flux. For example, a coniferous forest ecosystem in the Black Forest of Germany did not show any significant diurnal pattern of CH₄ flux due to the fact that this ecosystem has too small fluctuation in the diurnal dynamics of soil temperature (maximum 3.98 °C at the soil depth of 5 cm) to cause significant changes in CH₄ oxidation rates (Steinkamp et al., 2001).

A number of possible mechanisms were proposed to explain the diurnal variation in net methane flux in previous studies. First, higher temperature sensitivity of CH₄ production than CH₄ oxidation might account for diel variation in CH₄ flux (Castro et al., 1995; Dunfield et al., 1993; Steinkamp et al., 2001). Second, plant-mediated transport of CH₄ by diffusion and convective flow from soil to plant has diurnal variation, which might contribute to the diurnal pattern in CH₄ flux (Brix, 1992; Chanton et al., 1992; Joabsson et al., 1999; Kåki et al., 2001; Kim et al., 1998; Kowalska et al., 2013; Thomas et al., 1996; Van Der Nat et al., 1998). Third, diel variation in the physiological activity of stomatal conductance can be another mechanism that influences the diurnal pattern of CH₄ flux (Garnet et al., 2005; Schimel, 1995). Fourth, plant photosynthesis could influence the diurnal pattern of net methane flux by providing recently fixed carbon as a substrate for methanogenesis (Chanton et al., 1995; Joabsson et al., 1999; Ström et al., 2003).

In our study, in the nongrowing season, u^* and T_a were the dominant factors controlling the diurnal changes in net CH₄ flux (Table 1). This can be partly explained by the following mechanism. Field and lab studies have shown that the response of the methane oxidation rates to variations in soil temperature was strongest at low temperatures and became weak even negligible above a threshold of temperature (10 °C; Castro et al., 1995; Steinkamp et al., 2001). During the nighttime under relatively low temperature, the oxidation rates of CH₄ are higher than production rates and the ecosystem is characterized by net CH₄ uptake; as the temperature rises at daytime, the increasing methane production becomes more predominant, leading to a fluctuation up and down near zero. u^* and T_a also can control the diurnal changes in net CH₄ flux by influencing the diffusion of CH₄. Turbulence gets stronger as the temperature rises at daytime, which might benefit the transport of methane from soil to atmosphere. In summary, we suggest that lower temperature sensitivity of CH₄ oxidation and beneficial diffusion condition at daytime are the two major mechanisms accounting for the diurnal variation observed in net CH₄ flux during nongrowing season.

For the growing season, T_a and u^* were the dominant factors controlling the diurnal changes in net CH_4 flux (Table 1). This can be also explained by the first mechanism mentioned above. Since G_w and GPP did not have independent influence on the variation of net CH_4 flux (Figures S3e and S3f) and were not included in the ridge regression model, the third and fourth mechanisms may contribute little in this study. Anatomic studies on structures of different alpine plants have shown that most alpine plants have a well-developed aerenchyma (intercellular gaps, canal, or crevice) because of adaptation to the lack of oxygen on the Qinghai-Tibetan Plateau (He et al., 2007; Liu et al., 2009; Wu & Niu, 2017; Zhou et al., 1990; Zhou et al., 1992). In our study site, dominant species like *Taraxacum mongolicum*, *Aster alpinus* L., *Leontopodium leontopodioides*, *Potentilla anserina*, *Polygonum viviparum*, and *Ligularia virgaurea* all have advanced aerenchyma. So the second mechanism mentioned above, CH_4 transport from soil to atmosphere by diffusion at nighttime and additional plant-mediated convective flow transport by aerenchyma during daytime, may contribute to the diurnal dynamics of CH_4 flux in our study. However, there is little difference in net CH_4 flux variation at daytime between growing season and nongrowing season (Figure 2), so we suggest that the influence from plant-mediated transport on the diurnal pattern of net CH_4 flux is negligible during the growing season. In summary, same as the nongrowing season, we suggest that lower temperature sensitivity of methane oxidation and beneficial diffusion condition at daytime are the two major mechanisms accounting for the diurnal variation observed in net CH_4 flux during the growing season.

4.2. Seasonal Dynamic and Its Controls

We also detected a clear seasonal dynamic of CH_4 in this study, with higher uptake rates in summer and lower rates in winter. The similar seasonal variations of net CH_4 fluxes have been reported in alpine grasslands (Guo et al., 2016; He et al., 2014; Pei et al., 2003; Wang et al., 2009), temperate grasslands (Chen et al., 2010; Du et al., 1997; Du et al., 2005; Liu et al., 2007; Wang et al., 1998; Wang et al., 2000; Wang et al., 2013), and forests ecosystem (Steinkamp et al., 2001; Wei et al., 2018). In our study site, net CH_4 uptake occurred during the nongrowing season with freezing soil surface and low soil temperature, consistent with observations in a shortgrass steppe in North American (Mosier et al., 1996), an alpine grassland in the Qinghai-Tibetan Plateau (Pei et al., 2003), and a typical semiarid steppe grassland in Inner Mongolia (Wang et al., 2005). Contrasting to our observation, Wang et al. (2009) found, the alpine meadow was weak sink during the growing season but was neutral during the nongrowing season, probably due to higher altitude (4,600–4,800 m), deeper permafrost depth, thicker snow cover, and lower temperature during winter. No clear seasonal trend of the net methane uptake flux was found in a tropical rainforest in southern China due to its relatively high and stable soil temperature all year-round (Wei et al., 2018). This study suggested that the net CH_4 flux is highly dynamic at both diurnal and seasonal scales, which are predominately determined by the temporal changes in climate factors.

R_n was the most dominant factor controlling the seasonal changes in net CH_4 flux at our study site (Table 1). Bivariate regression results showed that T_{soil} at 10 cm and R_n were all negatively correlated with net CH_4 flux at the seasonal scale, but only R_n had a significant correlation with CH_4 flux in ridge regression (Figures 6 and S4 and Table 1). Therefore, solar radiation may control the seasonal variation in net CH_4 flux by influencing soil temperature and plant growth condition, which can be explained by the following mechanisms. First, higher radiation can increase CH_4 oxidation rate by increasing soil temperature. Second, radiation can also stimulate growth rate and abundance of methanotrophic microbes by enhancing temperature and C-substrates through increasing plant productivity. In addition, radiation can affect the plant-mediated transportation of CH_4 and O_2 from atmosphere to soil by affecting plant growth and ecosystem productivity, which influences net methane flux indirectly (Long et al., 2010). Similar to our results, Li et al. (2016) found that radiation promoted CH_4 uptake by releasing oxygen to the soil and providing abundant rhizosphere exudates that serve as oxidation substrates of methane through enhancing plant photosynthesis at a tundra ecosystem in the High Arctic. Soil temperature is generally considered to be a critical factor influencing seasonal patterns of net CH_4 uptake in both grassland and forest ecosystems (Chen et al., 2010; Liu et al., 2007; Wei et al., 2015; Wei et al., 2018). But our results indicated that the effects of temperature on the seasonal CH_4 uptake confounded with solar radiation. Although soil moisture is commonly considered a critical factor controlling methane production and oxidation, we found no correlation between soil moisture and the seasonal CH_4 uptake in this study. Our result differed from some other studies in grassland ecosystems (Bai et al., 2018; Dijkstra et al., 2013; Zhao et al., 2017), mainly due to that soil

moisture is not the most important limiting factor in alpine meadow as that in the temperate semiarid steppe.

Results of bivariate regression and partial regression in this study indicated that influences of different controlling factors on the diel and seasonal variation of net CH₄ flux are quite complex and difficult to distinguish. All the influencing factors had significant relationships with net CH₄ flux in the bivariate regression at the diurnal scale, but most were not significant in the partial regression. Especially for the analysis of diurnal variation in the nongrowing season, none of the factors were significant in the partial regression. This might be attributed to the confounding effects of different controlling variables. Most previous studies did not consider those confounding effects, causing conflicting results on the main drivers for CH₄ variation. Nevertheless, how to explicitly distinguish the influences of different controlling factors from each other need to be further explored in future studies.

4.3. Implications for Methane Budget Estimation

Only a few studies have estimated the methane sinks on the Qinghai-Tibetan Plateau with very limited data acquired from chamber observations, ranging from 0.19 to 0.28 Tg CH₄/year (Jin et al., 2015; Kato et al., 2011; Wang et al., 2014). In this study, our estimation showed that alpine meadows on the Qinghai-Tibetan Plateau acted as a strong net CH₄ sink with ~0.41-Tg CH₄/year uptake. The CH₄ uptake by alpine meadow on the Qinghai-Tibetan Plateau was higher than previous estimations mainly because the previous studies may neglect or underestimate CH₄ uptake in the nongrowing season. According to previous studies, the estimated CH₄ emissions of natural wetland ecosystems on the Qinghai-Tibetan Plateau range from 0.7 to 1.49 Tg CH₄/year (Chen et al., 2013; Jin et al., 1999; Jin et al., 2015). Our results showed that CH₄ consumption by alpine meadows can offset a relatively high portion of methane emissions from wetlands on the Qinghai-Tibetan Plateau. In fact, we only calculated the CH₄ uptake by alpine meadow. If alpine steppe was taken into consideration, alpine grassland might be a more considerable methane sink. Nevertheless, there has been no report or measurement of CH₄ consumption in the alpine grassland at ecosystem scale. So it is necessary to conduct field researches of methane fluxes in different ecosystems.

The temporal patterns and the determinants revealed in our observation may benefit the models to simulate the biosphere-atmosphere CH₄ exchange and estimate the methane budget. Explicit biological process-based models for methane consumption at the regional and global scales are difficult to formulate, due to large uncertainties in both structure and parameters (Bousquet et al., 2006; Curry, 2007; Smith et al., 2000). In this study we established regression models with high explanatory power between the net CH₄ flux and the controlling factors at different time scales (Table 1), which are useful for model validation, parameterization, structure improvement, and benchmark. On the other hand, because of sparse observation and lack of knowledge on the controlling mechanism of CH₄ variation, estimating the regional or global terrestrial methane sink remains a large challenge with large uncertainty (Curry, 2007; Kirschke et al., 2013; Lowe, 2006; Spahni et al., 2011; Tian et al., 2016). In this study we comprehensively revealed the mechanisms underlying the diurnal and seasonal dynamics of net CH₄ uptake at the ecosystem scale in an alpine meadow, which is of critical importance for methane budget estimation of Qinghai-Tibetan Plateau. Most previous studies only measured CH₄ flux a few times in a day or during a season, and these measurements were used to represent the average daily or seasonal CH₄ fluxes (Liu et al., 2017; Voigt et al., 2017; Wang et al., 2017; Zhao et al., 2017). However, using average values of a period in a day or a season to represent daily or annual methane fluxes may lead to large misestimation of CH₄ budget in ecosystems with highly variable diurnal and seasonal methane flux.

5. Conclusions

The alpine meadow ecosystem on the Qinghai-Tibetan Plateau acted as a strong methane sink and consumed about 0.41 Tg CH₄/year. An obvious diurnal dynamic characterized by a strong uptake in the nighttime and weak uptake in the daytime was observed in the net CH₄ flux during both the growing and nongrowing seasons. The net CH₄ flux was significantly higher in the growing season than in nongrowing season. The key controlling factors for the temporal dynamics varied with scales. The diurnal variation of net CH₄ flux was mainly explained by temperature and turbulence during the growing season ($R^2 = 0.83$) and the nongrowing season ($R^2 = 0.72$). The seasonal dynamics of CH₄ flux was best explained by the

combined effects of temperature and solar radiation ($R^2 = 0.49$). The findings in this study are crucial to attain better understanding of the mechanisms underlying the temporal variation of CH_4 flux and improving model predictions.

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