Seasonal and inter-annual variations in CO₂ fluxes over 10 years in an alpine shrubland on the Qinghai-Tibetan Plateau, China

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ABSTRACT

Alpine ecosystems play an important role in the global carbon cycle, yet the long-term response of *in situ* ground-based observations of carbon fluxes to climate change remains not fully understood. Here, we analyzed the continuous net ecosystem CO₂ exchange (NEE) measured with the eddy covariance technique over an alpine *Potentilla fruticosa* shrubland on the northeastern Qinghai-Tibetan Plateau from 2003 to 2012. The shrubland acted as a net CO₂ sink with a negative NEE ($-74.4 \pm 12.7 \text{ g C m}^{-2} \text{ year}^{-1}$, Mean $\pm$ S.E.). The mean annual gross primary productivity (GPP) and annual ecosystem respiration (RES) were 511.8 ± 11.3 and $437.4 \pm 17.8 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively. The classification and regression trees (CART) analysis showed that aggregated growing season degree days (GDD) was the predominant determinant on variations in monthly NEE and monthly GPP, including its effect on leaf area index (LAI, satellite-retrieved data). However, variations in monthly RES were determined much more strongly by LAI. Non-growing season soil temperature (T_s) and growing season length (GSL) accounted for 59% and 42% of variations in annual GPP and annual NEE, respectively. Growing season soil water content (SWC) exerted a positive linear influence on variations in annual RES ($r^2 = 0.40$, $p = 0.03$). The thermal conditions and soil water status during the onset of the growing season are crucial for inter-annual variations of carbon fluxes. Our results suggested that an extended growing season and warmer non-growing season would enhance carbon assimilation capacity in the alpine shrubland.

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1. Introduction

The cold and relatively humid climate in alpine ecosystems may facilitate soil carbon storage (Yang et al., 2010; Marcolla et al., 2011) and these ecosystems play an important role in the global carbon cycle with large proportion of labile carbon (Budge et al., 2011). Alpine ecosystems are also considered to be very sensitive to ongoing global warming (Wookey et al., 2009) and are coupled to the local climate system through various feedbacks (Piao et al., 2008; Barichivich et al., 2013; Ueyama et al., 2013; Shen et al., 2015a). Recent short-term observational studies have reported that the role of alpine ecosystems fluctuates between carbon sink, car-

bon neutral and carbon source, with large interannual variability and confounding abiotic and biotic effects (Kato et al., 2006; Li et al., 2006; Zhao et al., 2006; Reverter et al., 2010). However, their long-term carbon balance is still unclear because of non-linear metabolism processes and ecosystem plasticity responses to climate variability (Ma et al., 2007; Wohlfahrt et al., 2008a; Marcolla et al., 2011). Informed knowledge on the inter-annual variations in ground-based carbon fluxes for such ecosystems would improve our predictions of their potential responses to climate change (Piao et al., 2008, 2012).

The site-level temporal variations in a temperature-limited ecosystem carbon balance are believed to be regulated by thermal conditions (Kato et al., 2006; Zhao et al., 2006), water status (Yu et al., 2003; Marcolla et al., 2011), and vegetation phenology (Griffis et al., 2000; Ma et al., 2007; Shen et al., 2011), especially growing-season length (GSL) and aggregated growing degree days (GDD) (Groendahl et al., 2007; Barichivich et al., 2013; Ueyama

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et al., 2013), rather than some other single factors (Wohlfahrt et al., 2008a; Marcolla et al., 2011) or vegetation types (Kato et al., 2006; Street et al., 2007). In addition, pre-growing-season precipitation and temperature also played an important role in nutrient supply (Lafleur and Humphreys, 2007), vegetation phenology (Shen et al., 2015b), and vegetation photosynthetic performance during the following growing season (Griffis et al., 2000; Li et al., 2014). However, previous analyses of carbon balance have been limited to short-term observations (Kato et al., 2006; Zhao et al., 2006) or satellite measurements (Yu et al., 2003). Therefore, research based on multi-year *in situ* measurements could further our understanding of CO₂ fluxes in alpine ecosystems (Griffis et al., 2000; Marcolla et al., 2011).

Observational and manipulated studies in alpine regions have shown that warming advances the snow-melt date and green-up date, prolongs the growing season (Groendahl et al., 2007; Zhang et al., 2013), and promotes CO₂ assimilation and vegetation production in alpine ecosystems (Street et al., 2007; Li et al., 2015; Shen et al., 2015a). On the other hand, climate warming could enhance micro-organism activity and/or labile substrate availability, thereby stimulating soil C emissions, and depressing plant photosynthesis rate by limiting the soil water supply (Piao et al., 2008; Reverter et al., 2010; Chen et al., 2016). The balance between these opposing biological mechanisms determines how alpine ecosystems affect the climate system, but little observational evidence exists to assess their effects. The related long-term *in situ* ground-based flux data are useful (Griffis et al., 2000; Marcolla et al., 2011), while few data on alpine ecosystems over the Qinghai-Tibetan Plateau (QTP) are available (Yang et al., 2010). The QTP has experienced substantial warming in recent decades (Piao et al., 2011; Shen et al., 2015a) and knowledge of the long-term ecosystem carbon balance response of alpine shrubland remains limited (Li et al., 2006; Zhao et al., 2006). It is possible that a warmth-induced expansion in the range of alpine shrubland could cause changes in soil carbon storage and regional CO₂ budgets (Sturm et al., 2005). Therefore, in this study we present 10 years of continuous flux data, obtained using the eddy covariance (EC) technique in alpine shrubland on the northeastern QTP, from January 2003 to December 2012. The objectives of this study were: (1) to quantify the seasonal and inter-annual variability of net ecosystem CO₂ exchange (NEE), ecosystem respiration (RES), and gross primary production (GPP); and (2) to clarify the major environmental factors controlling the variations in seasonal and annual CO₂ fluxes. We hypothesized that seasonal CO₂ fluxes would be controlled by thermal conditions while inter-annual CO₂ fluxes would be regulated by growing season length (Kato et al., 2006; Ueyama et al., 2013).

2. Materials and methods

2.1. Site description

The study site is located in an alpine *Potentilla fruticosa* shrubland, near the Haibei National Field Research Station for Alpine Grassland, Qinghai (37°36'N, 101°19'E, 3200 m a.s.l.), on the northeastern QTP in a region of alpine permafrost. This region has a plateau continental climate with evident cold-dry (from November to following April) and warm-wet (from May to October) seasons. Based on meteorological data from 1980 to 2010, the mean annual air temperature (T_a) is about -1.0°C ; the warmest monthly T_a is approximately 10°C in July and the coldest is approximately -15°C in January. Mean annual precipitation is approximately 580 mm, of which 80% is concentrated in the warm-wet season (Li et al., 2006; Zhao et al., 2006). The depth of permafrost in the studied region

is about 6 m and overall is in a state of degradation (Wang et al., 2015).

The vegetation canopy of the alpine *Potentilla fruticosa* shrubland ecosystem consists of two layers with shrubs and grasses. The primary layer is mainly formed by *Potentilla fruticosa* shrubs. The canopy height and shrub coverage is approximately 30–60 cm and 60%–80%, respectively. The secondary layer of grass is composed of dominant species *Kobresia humilis*, *Stipa aliena*, *Poa orinosa*, *Helictotrichon tibeticum*, *Elymus nutans*, *Aster flaccidus*, *Polygonum viviparum*, and *Leontopodium nanum*, with approximately 8–16 cm vegetation canopy height and 70%–80% plant coverage fraction during peak growing season (July and August). Soil is a clay loam and classified as Mollic Gric Cambisols, featuring high levels of organic matter and low levels of available nutrients (soil organic matters up to 106.7% and available nitrogen 0.039% in the 0–10 cm soil layer: personal observational data). According to the phenology of most of flora in alpine shrublands, the growing season (from a flux data processing perspective) is defined as April 20–October 10 (Zhao et al., 2006). Meanwhile, based on a plant-centric year rather than the calendar year (Robinson et al., 2013; Li et al., 2015), last October 11–April 19 is classified as the non-growing season of the current year. However, the non-growing season in 2003 only covered January 1–April 19 due to a lack of data. The study sites are lightly ($3.75 \text{ sheep ha}^{-1}$) grazed by yak and Tibetan sheep during the non-growing season.

2.2. Flux and climatic factors measurements

An open-path eddy covariance (EC) system was installed in the center of a fairly flat (slope < 1%), open (5 km minimum distance from mountain base) and homogenous vegetated area (average shrub coverage 70%) covering about 12 km². The EC system consisted of a three-dimensional ultrasonic anemometer (CSAT3, Campbell, USA) and an open-path infrared CO₂/H₂O gas analyzer (LI-7500, LI-Cor, USA), both fixed at a height of 2.2 m above the ground. The raw data (wind speed, sonic virtual temperature, and CO₂ and H₂O concentrations) were sampled at 10 Hz. The 30-min fluxes were calculated, adjusted by WPL (Webb, Pearman and Leuning) density correlation, and logged with a data logger (CR5000, Campbell, USA). The CO₂/H₂O gas analyzer was calibrated during the end of each April. Zero points, CO₂ span and water span were established using dry N₂ gas (99.999%, National Institute of Metrology, China), standard CO₂ gas (450 mg/kg, National Institute of Metrology, China) and a dew-point generator (LI-610, LI-Cor, USA), respectively.

The routine meteorological factors were measured synchronously. Air temperature (T_a) and relative humidity were monitored by a temperature and humidity probe (HMP45C, Vaisala, Finland) at both 1.5 m and 2.5 m, and were used to estimate vapor pressure deficit (VPD). Wind speed and direction were sampled by a cup anemometer (034A-L, RM Young, USA) and a dogvane (014A, RM Young, USA) at a height of 2.5 m. Shrub canopy temperature was measured via infrared thermocouple sensor (IRTS-P, Apogee, UT) at 1.5 m. Radiation (including downward long-wave and short-wave, upward long-wave and short-wave radiation) and photosynthetic photon flux density (PPFD) were monitored with 4 radiometers (CM11, Kipp & Zonen, Netherlands) and a quantum sensor (LI-190SB, LI-Cor, USA), respectively, at 1.5 m height. Precipitation was collected with a rain gauge (52203, RM Young, USA) installed at 0.5 m above ground level. Using thermocouple probes (105T, Campbell, USA), soil temperature was measured at depths of 5, 10, 20, 40, and 80 cm. Volumetric soil water content was monitored by time-domain reflectometry (CS616, Campbell, USA) at 10 and 20 cm depths. The soil heat flux was measured with heat plates (HFT-3, Campbell, USA) buried at three different points at 1 cm below the soil surface. Thirty-minute averages of meteorological

data were recorded with a data logger (CR23XTD, Campbell, USA). The system energy closure ratio (defined as the ratio between the sums of turbulent and soil heat fluxes against radiant fluxes) was above 75% (Zhao et al., 2006), which indicated that flux measurements were reasonable.

The amplitude of the diurnal temperature range (ADT, defined as the difference between average daytime air temperature (T_a) and average nocturnal T_a) was calculated. Growing-season length (GSL) and aggregated growing degree days (GDD) were defined as the lengths and aggregated degree days, respectively, for periods when daily T_a was above 5 °C for at least five consecutive days (Marcolla et al., 2011). Similarly, chilling degree days (CDD) was based on soil temperature (T_s) and is a negative value defined as the sum of daily T_s values below 0 °C during the non-growing season (Shen et al., 2015b).

2.3. Satellite leaf area index

Remotely sensed leaf area index (LAI) products (MOD15A2) were used in this study to analyze the effects of LAI on carbon fluxes. LAI is retrieved every 8 days at 1 km resolution, and obtained from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC, <http://daac.ornl.gov/MODIS/modis.html>). Each LAI image was sampled by selecting the pixel covering the flux tower. Although LAI was not zero and was somewhat unreliable during the non-growing season, values were retained to ensure data integrity. These satellite-derived LAI data for estimating shrubland green leaf quantity compared very favorably with the half-monthly LAI (LAI_m) of nested grassland among shrubland ($LAI = 1.15LAI_m - 0.15$, $r^2 = 0.73$, $p < 0.001$), which was measured using a LI-3000 portable leaf area meter (LI-COR, USA) after grass harvesting in 5 replicate 50 × 50 cm quadrats during the growing season (unpublished data from 2005 to 2007). For comparison with the flux data, mean monthly values of LAI were used for the subsequent analyses.

2.4. Data quality control, gap filling, flux partitioning

Corrections for axis rotation, trend removal and storage item were not applied to the raw eddy data because the small bias is likely to be negligible in our flat study sites with low plant canopy height (Kato et al., 2006; Zhao et al., 2006). Because of the low fragmentation induced by dwarf shrubs, there was little contribution to the fluxes at frequencies greater than 1 Hz, indicating that the sampling frequencies were adequate with no loss of high-frequency fluxes at about four-fold canopy measurement heights (Fu et al., 2009). The standard methodologies for flux data processing recommended by ChinaFLUX were applied (Yu et al., 2008). The 30-min flux data (NEE) were removed during precipitation or when the absolute value of NEE was above 1.0 mg CO₂ m⁻² s⁻¹. Meanwhile, NEE was assumed to be normally distributed and rejected by the filter $|NEE - \bar{NEE}| > 4.5\delta_{NEE}$ (NEE and δ_{NEE} are the mean value and standard deviation of NEE) using a 10-day moving window. The night-time (PPFD < 10 μmol m⁻² s⁻¹) CO₂ flux data collected under low atmospheric turbulence conditions were screened using thresholds of friction velocity (u_*), and flux data were removed when $u_* < 0.15$ m s⁻¹. During the non-growing season, spurious CO₂ absorption measurements were mainly induced by self-heating of the open path CO₂/H₂O infrared sensor, and negative CO₂ flux data (representing what the ecosystem absorbed from the atmosphere) were discarded. Meteorological data lying outside of the minimum or maximum thresholds (based on meteorological data from 1980 to 2010 of Haibei weather station) were removed.

The gaps in meteorological data were filled by temporal linear interpolation. Radiation data were parameterized as a function of time, elevation, location, and atmospheric transparency coeffi-

cients in order to fill missing values. The missing CO₂ flux data were filled using a non-linear function of environmental variables and valid flux data: specifically, the night-time flux gaps were filled using the enhanced Van't Hoff equation (Yu et al., 2008) (Eq. (1)), which considers 5-cm soil temperature (T_s) and 10-cm volumetric soil water content (SWC). Daytime flux gaps were filled by a rectangular hyperbolic light-response function (Eq. (2)) during the growing season (April 20–October 10) and by Eq. (1) during the non-growing season, on the assumption that the relationship between night-time NEE and soil temperature holds during the daytime (Ma et al., 2007; Yu et al., 2008). We note that this assumption may introduce a potential error. The two equations are:

$$R_{eco,n} = R_{eco,ref} e^{\ln(a+bT_s+cSWC+dSWC^2)(T_s-10)/10} \quad (1)$$

$$NEE = R_{eco,d} - \frac{a \times P_{max} \times PPFD}{P_{max} + a \times PPFD} \quad (2)$$

where $R_{eco,ref}$ is the reference ecosystem respiration rate when soil temperature is 10 °C; $R_{eco,d}$ is ecosystem dark respiration rate, and a and P_{max} are the apparent quantum yield and saturated photosynthesis rate. Best-fit parameters a , b , c , d in Eq. (1) and $R_{eco,d}$, a , P_{max} in Eq. (2) were calculated using valid flux data and a 5-day moving window in Matlab R2007a (Mathworks Inc., USA). With the exception of power failure in the entire month of September 2005, available data for the other 9 years comprise approximately 82% of daytime records (75% for 2005).

We partitioned daily NEE into daily GPP and daily RES by the following method (Eq. (3)). Daily RES was the sum of daytime respiration (RES_d) and nocturnal respiration (RES_n), where RES_d was estimated and extrapolated by Eq. (1) (Groendahl et al., 2007) based on the diurnal values of T_s and SWC. Daily GPP was obtained by subtracting RES from NEE, as shown in the following equation (Eq. (3)). Negative and positive NEE represented CO₂ absorption and release by the ecosystem, respectively (Yu et al., 2008).

$$GPP = RES - NEE = (RES_d + RES_n) - NEE \quad (3)$$

2.5. Statistical analysis

Because of collinearities and nonlinearities among ecological variables, classification and regression tree (CART) analysis was adopted, which is a machine-learning algorithm capable of identifying relatively important relevant variables without the need for transformations or assumption on variable distribution or observation independence. CART is a graph-based, nonparametric model, permitting much easier exploration and understanding than traditional statistical techniques. Essentially, a CART model derives prediction rules by dividing the predictor variable space into rectangular subspaces, with each subspace being assigned a single response variable value (De'Ath and Fabricius, 2000). Therefore, CART was employed to identify the main environmental controlling factors (air and soil temperature, photosynthetic photon flux density, volumetric soil water content, amplitude of diurnal temperature, precipitation, vapor pressure deficit, leaf area index, and aggregated growing degree days) on variations of monthly GPP, RES and NEE. In the CART model, the proportional reduction in error (PRE) is equivalent to a traditional coefficient of determination (r^2) and is used to judge the model performance. The maximum number of splits and the minimum PRE were set to 5 and 0.01, respectively. Linear regression was used to assess the inter-annual impacts of environmental factors on annual variations of CO₂ fluxes. The CART and linear regression analyses were performed in SYSTAT 13.0 (Systatsoftware Inc, USA).

Fig. 1. Anomaly of annual air temperature, annual precipitation and annual CO₂ fluxes.

3. Results

3.1. Variations in annual climate and leaf area index

Based solely on a threshold of a 20% deviation from the mean annual air temperature (T_a), the years 2003, 2007, 2009, 2010

and 2012 were relatively warm ($>0.8T_a$) while 2005, 2006, 2011 and 2004, 2008, 2012 were classified as normal years and cooler years ($<1.2T_a$) respectively (Fig. 1). Annual precipitation (Rain) was 461.0 mm, ranging from 342.4 mm (2008) to 546.1 mm (2003). The years 2003, 2005, 2011 were wetter years (>1.1 Rain) 2008, 2012 were drier years (<0.9 Rain) (Table 1). Annual volumetric soil water

Table 1
Annual air temperature (T_a , °C), precipitation (Rain, mm), gross primary production (GPP, $\text{g C m}^{-2} \text{ year}^{-1}$), ecosystem respiration (RES, $\text{g C m}^{-2} \text{ year}^{-1}$), and net ecosystem exchange (NEE, $\text{g C m}^{-2} \text{ year}^{-1}$) of alpine shrubland from 2003 to 2012. Negative fluxes represent a net carbon uptake by the ecosystem.

Periods		T_a	Rain	GPP	RES	NEE
2003 ^b	Year	−0.9h	546.1w	418.8	408.1	−10.6
	Growing	5.0h	507.9w	418.8	369.4	−49.3
	Non-growing ^a	−8.8n	26.5w		24.2	24.2
2004	Year	−1.9c	493.5n	461.9	363.4	−98.5
	Growing	4.3n	461.5n	461.9	333.5	−128.4
	Non-growing	−10.3n	37.2w		31.4	31.4
2005	Year	−1.3n	523.2w	466.3	365.8	−100.6
	Growing	4.9n	494.7w	466.3	332.0	−134.3
	Non-growing	−9.9n	28.2w		32.5	32.5
2006	Year	−1.6c	426.1n	545.0	519.6	−27.4
	Growing	4.3n	420.4n	545.0	474.2	−72.7
	Non-growing	−10.2n	8.3d		38.7	38.7
2007	Year	−0.9h	442.9n	522.0	458.2	−63.7
	Growing	5.2n	417.5n	522.0	432.2	−89.8
	Non-growing	−9.7n	27.7w		35.0	35.0
2008	Year	−1.9c	342.4d	525.7	471.2	−54.5
	Growing	4.1n	329.8d	525.7	446.3	−79.4
	Non-growing	−10.4n	14.4d		27.0	27.0
2009	Year	−0.7h	457.1n	598.4	471.1	−127.2
	Growing	5.2n	441.4n	598.4	440.3	−158.0
	Non-growing	−8.2n	13.6d		25.3	25.3
2010	Year	−0.8h	447.4n	501.2	369.1	−132.0
	Growing	5.2n	433.6n	501.2	337.7	−163.5
	Non-growing	−9.5n	15.8d		33.4	33.4
2011	Year	−1.5n	531.9w	543.1	487.1	−56.0
	Growing	5.0n	504.2w	543.1	455.0	−88.0
	Non-growing	−10.7n	18.2d		26.4	26.4
2012	Year	−1.7c	399.2d	533.7	460.5	−73.2
	Growing	4.7n	380.4d	533.7	430.9	−102.8
	Non-growing	−10.7n	26.1w		33.0	33.0
Mean ± S.E.	Year	−1.3 ± 0.1	461.0 ± 20.2	511.8 ± 16.3	437.4 ± 17.8	−74.4 ± 12.7
	Growing	4.8 ± 0.1	439.14 ± 17.89	511.8 ± 16.3	405.2 ± 17.6	−106.6 ± 12.0
	Non-growing	−9.9 ± 0.2	21.84 ± 3.2		32.3 ± 1.9	32.3 ± 1.9
Coefficient of variance	Year	35.3%	13.9%	10.0%	12.9%	54.0%
	Growing	2.7%	4.1%	10.0%	4.3%	11.3%
	Non-growing	2.2%	14.6%		5.9%	5.9%

^a Non-growing season is from last October 21 to April 19 based on the plant-centric year.

^b Non-growing season in 2003 from January 1 to April 19 because of lack available data, letter behind T_a and Rain represents h (hot), normal (n), cool (c) and w (wet), n (normal) and d (dry), respectively.

content (SWC) was not correlated with annual Rain ($r^2 = 0$, $p = 0.93$). Annual leaf area index (LAI) peaked at 1.48 under the cooler and wetter conditions in 2011, and was not directly controlled by T_a ($p = 0.62$), Rain ($p = 0.78$) or SWC ($p = 0.41$).

3.2. Seasonal and inter-annual variations of GPP, RES and NEE

Monthly GPP ($163.1 \pm 5.6 \text{ g C m}^{-2} \text{ month}^{-1}$) and monthly NEE ($-72.3 \pm 4.1 \text{ g C m}^{-2} \text{ month}^{-1}$, mean $\pm$ S.E., with the same notation hereon in) peaked in July while maximum monthly RES occurred in July ($90.8 \pm 5.3 \text{ g C m}^{-2} \text{ month}^{-1}$) and August ($90.7 \pm 4.8 \text{ g C m}^{-2} \text{ month}^{-1}$). Linear regression suggested that the variations in monthly NEE were controlled mainly by monthly GPP ($r^2 = 0.92$, $p < 0.01$) rather than monthly RES ($r^2 = 0.65$, $p < 0.01$) during the growing season.

Annual GPP and annual RES were $511.8 \pm 11.3 \text{ g C m}^{-2} \text{ year}^{-1}$ and $437.4 \pm 17.8 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively (Table 1). Variability in annual GPP and annual RES was predominantly determined by monthly GPP ($r^2 = 0.84$, $p < 0.01$) and monthly RES ($r^2 = 0.96$, $p < 0.01$) in the peak growing season (July and August). The 10-year average NEE was $-74.4 \pm 12.7 \text{ g C m}^{-2} \text{ year}^{-1}$ with a high annual coefficient of variance (CV, 54%) and a range of $-132.0 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2010 to $-10.6 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003. The variations in annual NEE were also controlled by monthly NEE during the peak growing season ($r^2 = 0.77$, $p < 0.001$). These findings suggested that peak growing seasonal CO_2 fluxes played a predominant role in variations in annual carbon balance of the alpine shrubland.

Variations in annual NEE were not directly controlled by either RES ($p = 0.15$) or annual GPP ($p = 0.47$). The average annual ratio of RES/GPP was 0.86 ± 0.025 , which was to some extent controlled by RES ($r^2 = 0.37$, $p = 0.06$) than by GPP ($r^2 = 0.01$, $p = 0.79$). Additionally, we did not observe a significant difference between annual CO_2 fluxes under different temperature ($p > 0.80$; warmer, normal and cooler) or precipitation ($p > 0.40$; wetter, normal and drier) classifications. However, it seemed that annual RES ($p = 0.08$) and annual GPP ($p = 0.16$) were both depressed during wetter years, except 2011 for RES and 2010 for GPP (Fig. 1).

3.3. Response of seasonal variations of GPP, RES and NEE to environmental factors

The proportional reduction in error (PRE) was above 0.94 and indicated a good performance of classification and regression trees for monthly CO_2 fluxes. Monthly aggregated growing degree days (GDD) was the most important determinant and explained 79% and 82% variations of monthly GPP (Fig. 2a) and NEE (Fig. 2c), respectively. The split values of GDD were both about 170°Cd , which occurred at the end of May or middle of September. The split values of GDD on the second left node occurred in the beginning of July or middle of August, suggesting that monthly GPP and NEE was mainly determined by thermal conditions during the plants' peak growing stage. Over the full growth period, GPP ($r^2 = 0.36$, $p = 0.003$, $n = 20$) and NEE ($r^2 = 0.22$, $p = 0.02$, $n = 20$) were enhanced under higher VPD. The variable of the second right root node was LAI for GPP, which indicated biotic factors played an important role in ecosystem photosynthetic activity during the vegetation re-greening and withering periods. However, for the corresponding important variable for NEE was soil temperature, suggesting that carbon balance was controlled by RES during that stage (Fig. 2b). Overall, monthly GDD showed a stronger influence on variations in monthly GPP than that of RES ($p < 0.001$, Fig. 3) during the growing season, in addition noting its positive linear influence on monthly LAI ($r^2 = 0.77$, $p < 0.001$), which also significantly correlated with monthly GPP (Fig. 4). Meanwhile, partial correlation also confirmed

Fig. 2. Regression trees for monthly CO_2 fluxes from environmental variables.

Fig. 3. The relationship between monthly CO₂ fluxes and aggregated growing season degree day.

Fig. 4. Correlation of monthly CO₂ fluxes with monthly leaf area index during growing season.

the slightly stronger effect of GDD on GPP ($r = 0.75$, $p < 0.001$) and NEE ($r = 0.70$, $p < 0.001$) than that of LAI.

Monthly LAI played a much more important role in regulating variations of monthly RES (Fig. 2b). The left part of the first node represented RES in the non-growing season, and the initial (last) vegetation growth stage was strongly influenced by soil temperature (T_s). Monthly LAI regulated monthly RES at the beginning and end stages, while photosynthetic photon flux density promoted monthly RES at the middle stage of the growing season. Thus, monthly LAI determined monthly RES (Fig. 4) during the peak growing season while monthly RES was positively exponentially related with monthly T_s ($RES = 6.05e^{\ln(4.42)(T_s + 4.20)/10}$, $r^2 = 0.84$, $p < 0.001$) during other times. Furthermore, the residual analysis showed that LAI had a significant influence on RES residuals from the T_s exponential function ($RES_{rt} = 4.35LAI - 6.13$, $r^2 = 0.06$, $p = 0.02$), while T_s had no influence ($RES_{rt} = 0.37T_s - 2.84$, $r^2 = 0.003$, $p = 0.27$).

Higher diurnal temperatures promoted higher production while lower nocturnal temperatures depressed ecosystem respiration on the Plateau (Zhao et al., 2006). However, there was little correlation between monthly amplitude of diurnal temperature (ADT) and monthly GPP ($r^2 = 0.01$, $p = 0.23$) or monthly NEE ($r^2 = 0.02$, $p = 0.15$). Only monthly RES was depressed by monthly ADT ($r^2 = 0.11$, $p < 0.01$) mainly due to its effect in the non-growing season

($r^2 = 0.14$, $p = 0.007$) rather than in the growing season ($r^2 = 0.01$, $p = 0.22$), suggesting that ADT exerts a negligible influence on seasonal CO₂ fluxes in the alpine shrubland.

3.4. Response of annual GPP, RES and NEE to environmental factors

Annual soil temperature (T_s) and annual photosynthetic photon flux density exhibited significant influences on variations in annual GPP (Table 2), with stepwise regression showing that the non-growing season T_s played a much more important role in the variations in annual GPP (Fig. 5a). It is worth noting that October T_s correlated with GPP of the following July ($r^2 = 0.41$, $p = 0.04$, $n = 9$), suggesting that a warmer autumn facilitated starch storage and promoted photosynthetic activity of perennial plants in the following season. Annual RES was positively correlated with annual soil water content (SWC, Table 2), specifically SWC in May (Fig. 5b) or in the growing season ($r^2 = 0.40$, $p = 0.03$). The annual RES response to annual aggregated growing degree days (GDD) could be described as a parabolic curve with an optimum GDD of $1038^\circ\text{C}\cdot\text{d}$ ($RES = -0.0066\text{GDD}^2 + 13.7\text{GDD} - 6643.4$, $r^2 = 0.41$, $p = 0.066$). Annual NEE was regulated by annual growing season length (GSL, Table 2), most specifically the starting date of the growing season (Fig. 5c). Moreover, most variations (52%) in annual NEE were explained by vapor pressure deficit (VPD) and GSL ($NEE = -2.33\text{GSL} - 809.38\text{VPD} + 478.75$, $p = 0.032$). Annual NEE also exhibited a parabolic response to GDD ($NEE = -0.0036\text{GDD}^2 + 7.2\text{GDD} - 3650.9$, $r^2 = 0.56$, $p = 0.023$), suggesting that annual RES rather than GPP might have played a more important role in annual NEE. Overall, annual T_s was the most important variable for describing variations in annual GPP while annual SWC regulated variations in annual RES.

4. Discussion

4.1. Growing season variations of GPP, RES and NEE

Consistent with our hypothesis, aggregated growing degree days (GDD), and to a lesser extent soil temperature (T_s), played a predominant role in regulating the variations in monthly NEE and monthly GPP in the alpine shrubland (Figs. 2 and 3). This pattern probably occurred because the direct effect of growing season temperature on plant photosynthetic performance was stronger in the alpine ecosystem where this is greater above-ground biomass (Reverter et al., 2010; Ueyama et al., 2013; Shen et al., 2015a), and the cumulative effect of temperature was the principal limiting factor in breaking plant dormancy, leaf phenological development and subsequent plant growth (Kato et al., 2006; Marcolla et al., 2011; Shen et al., 2015b). Consequently, alpine plants have ample phenotypic plasticity in their metabolism, particularly in regard to temperature (Körner, 1999). Additionally, thermal conditions were indirectly positively correlated with the available nutrient supply through soil microbial and enzyme activity under sufficient water conditions (Wohlfahrt et al., 2008b), thereby providing a key control on ecosystem photosynthesis at certain canopy LAI levels in a temperature-limited environment (Street et al., 2007).

The monthly variations in growing-season RES were much more strongly determined by LAI than by temperature (Fig. 2b). This agrees well with dominance of total autotrophic respiration on carbon effluxes in the alpine ecosystem during the plant growing season (Griffis et al., 2000; Street et al., 2007; Chen et al., 2016). First, the high vegetation canopy coverage (>95%) and aboveground biomass (Fig. 6) indicated strong vegetation autotrophic respiration (Fu et al., 2009), contributing more than 75% of the alpine meadow

Table 2

Linear regressions between annual gross primary production (GPP, $\text{g C m}^{-2} \text{ year}^{-1}$), ecosystem respiration (RES, $\text{g C m}^{-2} \text{ year}^{-1}$), and net ecosystem exchange (NEE, $\text{g C m}^{-2} \text{ year}^{-1}$) and annual environmental factors, including air temperature (T_a , $^{\circ}\text{C}$), precipitation (Rain, mm), soil water content (SWC, $\text{cm}^3 \text{ cm}^{-3}$) and leaf area index (LAI, $\text{m}^2 \text{ m}^{-2}$), growing season length (GSL, d), aggregated growing season degree days (GDD, $^{\circ}\text{C d}$).

Factor	GPP			RES			NEE		
	Linear Equation	r^2	p	Linear Equation	r^2	p	Linear Equation	r^2	p
T_a (x_1)	$y = 14.84x_1 + 530.42$	0.00	0.74	$y = -8.72x_1 + 426.48$	0.00	0.86	$y = -23.56x_1 - 103.95$	0.00	0.50
PPFD (x_2)	$y = -0.89x_2 + 788.95$	0.36	0.04	$y = -0.88x_2 + 709.67$	0.26	0.07	$y = 0.016x_2 - 79.28$	0.00	0.97
T_s (x_3)	$y = 66.93x_3 + 329.56$	0.41	0.03	$y = 0.078x_3 + 0.34$	0.00	0.46	$y = -38.81x_3 + 31.31$	0.17	0.13
SWC (x_4)	$y = 1215.59x_4 + 257.84$	0.11	0.18	$y = 1854.10x_4 + 50.09$	0.33	0.05	$y = 638.51x_4 - 207.75$	0.00	0.39
Rain (x_5)	$y = -0.40x_5 + 696.45$	0.15	0.14	$y = -0.37x_5 + 609.06$	0.08	0.22	$y = 0.028x_5 - 87.39$	0.00	0.90
VPD (x_6)	$y = 414.31x_6 + 398.80$	0.00	0.66	$y = -787.14x_6 + 652.08$	0.00	0.44	$y = -1201.46x_6 + 253.28$	0.27	0.07
LAI (x_7)	$y = 192.84x_7 + 376.32$	0.05	0.26	$y = 140.55x_7 - 338.69$	0.00	0.47	$y = -52.29x_7 - 37.63$	0.00	0.71
GSL (x_8)	$y = 2.90x_8 + 98.27$	0.21	0.10	$y = -0.0054x_8 + 438.21$	0.00	0.99	$y = -2.91x_8 + 339.92$	0.42	0.025
GDD (x_9)	$y = 0.23x_9 + 268.94$	0.02	0.30	$y = -0.062x_9 + 502.31$	0.01	0.81	$y = -0.29x_9 + 233.37$	0.27	0.07

Note: the bolded equations represented significance of regression results at the level of $p < 0.05$.

Fig. 5. The relationship between annual CO_2 fluxes and soil temperature, soil water content and start date of growing season.

Fig. 6. The relationship between annual NEE and grass ANPP and shrub ANPP.

ecosystem respiration (Chen et al., 2016). Second, the heterotrophic respiration was directly controlled by microbial biomass carbon and substrate availability, which was partially influenced by the plant photosynthetic production (McFadden et al., 2003; Marcolla et al., 2011). Indeed, a highly significant correlation was found

between monthly RES and monthly GPP during the growing season ($r^2 = 0.69, p < 0.001$). Consequently, variations in the growing season NEE were much more strongly determined by GPP than by RES, consistent with reports that NEE was GPP-dependent in other temperature-limited ecosystems (McFadden et al., 2003; Sturm et al., 2005; Groendahl et al., 2007; Ueyama et al., 2013).

Water status (precipitation or soil water content) exerted a minor influence on variations in monthly CO_2 fluxes. This is consistent with the almost complete absence of drought stress even during the peak growing season in our alpine shrubland (Fu et al., 2006, 2009), and might be the consequence of the high water holding-capacity in this clay loam with a high soil organic matter content ($>10\%$) and good water supply synchronized with precipitation in summer (Li et al., 2015). Furthermore, there might be little moisture competition between deep-root shrubs and shallow-root grasses (Street et al., 2007), as partially supported by the findings that a greater VPD promoted monthly GPP when GDD was above 250°C d (Figs. 2a and c).

4.2. Inter-annual variations of GPP, RES and NEE

Soil temperature (T_s) in the non-growing season played an important role in variations of following-season annual GPP (Fig. 5). This was a cumulative effect, as indicated by the negative linear

correlation between annual GPP and chilling degree days of T_s ($r^2 = 0.51$, $p = 0.01$). This may be because a warming non-growing season promoted faster litter decomposition, and the resulting presence of greater nutrient supplies (especially available nutrients) (Hobbie and Chapin, 1996) would favor more rapid vegetation recovery and growth in a non-water-limited ecosystem (Yu et al., 2003; Sturm et al., 2005; Shen et al., 2011). Indirectly, a warmer soil temperature during the non-growing season advanced the snow melting date and reduced surface albedo, consequently advancing the re-greening date (Pettorelli et al., 2005; Reverter et al., 2010) and therefore prolonging the growing season (Groendahl et al., 2007; Zhang et al., 2013) and strengthening vegetation activities (Yu et al., 2003). This would promote carbon sequestration in the humid alpine ecosystem (Lafleur and Humphreys, 2007; Piao et al., 2008; Li et al., 2014). Meanwhile, we also found significant correlation ($r^2 = 0.36$, $p = 0.04$) between growing season length and T_s of the non-growing season.

Annual RES was significantly controlled by annual soil water content (SWC, Table 2). Although we are aware that strong statistical correlation does not imply causality, a possible reason is that greater SWC during the growing season could weaken the thermal acclimation of heterotrophic respiration and maintenance respiration in alpine meadow (as shown in a warming experiment by Chen et al., 2016). In support of this hypothesis, RES declined when GDD was above 1038 °C d. Soil moisture dynamics in May were characterized by freeze-thaw cycles during the green-up periods (Groendahl et al., 2007; Barichivich et al., 2013) and were indicative of water availability for sustaining the spring recovery of vegetation (Shen et al., 2011); May soil moisture accounted for 55% of variations in annual RES (Fig. 5b) and 32% of annual GPP ($p = 0.05$). To some extent this supports how the timing of growing season onset (Lafleur and Humphreys, 2007; Shen et al., 2011) and soil water status can play a positive role in vegetation activity in alpine grassland ecosystems (Robinson et al., 2013; Shen et al., 2015b).

The starting date of growing season length (GSL) regulated the variation in annual NEE, which indicated that thermal conditions at the onset of the growing season were critical for triggering the emergence of leaves (Griffis et al., 2000; Kato et al., 2006; Ma et al., 2007; Marcolla et al., 2011), and were much more important than water status in determining ecosystem carbon assimilation capacity (Yu et al., 2003; Groendahl et al., 2007; Barichivich et al., 2013). The potential underlying mechanism is that the lower risk of drought allows alpine plants to maximize the thermal benefits in our humid region (Yu et al., 2003; Shen et al., 2015b). Moreover, early re-greening could increase photosynthesis more than respiration (Kato et al., 2006; Piao et al., 2008), and we also found that monthly GDD stimulated monthly GPP (slope = 0.36, $r^2 = 0.53$, $p = 0.01$) much more strongly than monthly RES (slope = 0.22, $r^2 = 0.29$, $p = 0.06$) during May. Additionally, annual NEE of the adjacent alpine meadow was $-120.9 \pm 36.0 \text{ g C m}^{-2} \text{ year}^{-1}$ (Kato et al., 2006), which was higher than that of shrubland and indicated that the shrub expansion would reduce alpine meadow ecosystem carbon sink strength by increasing RES by 17% and reducing GPP by 24%. Consistent with these findings, nested-grass above-ground net primary production (ANPP), rather than shrub ANPP (green branches, buds and flowers), as measured by destructive harvesting with 5 replicates for grass and 3 for shrubs from 2008 to 2012, correlated well with annual NEE (Fig. 6). However, higher C/N ratios of shrub woody stems and root residuals, with long turnover times, should slow soil decomposition rate (Sturm et al., 2005; Budge et al., 2011) and therefore ecosystem respiration, resulting in complex biogeochemical drivers of litter decomposition and soil feedbacks to shrub expansion if increasing RES does occur. Further manipulation experiments are needed to explore this clearly.

5. Conclusions

The 10-year continuous times series of CO_2 fluxes measured with the eddy covariance technique in the alpine shrubland ecosystem on the northeastern Qinghai-Tibetan Plateau from 2003 to 2012 showed that the alpine shrubland acted as a weak carbon sink with high inter-annual variability. Aggregated growing season degree day and satellite-derived leaf area index played dominant roles in regulating seasonal variations of CO_2 fluxes. The thermal conditions (soil temperature, growing season length) and soil water status determined inter-annual variations of CO_2 fluxes. Our findings indicate that both thermal and moisture conditions during the onset of the growing season played important roles in variations in annual carbon balance in the alpine shrubland. We speculate that the warming scenario, especially non-growing season warming and a prolonged growing season, would enhance the carbon sink strength of alpine shrubland on the Qinghai-Tibetan Plateau unless there is a deficit in water availability. However, shrub expansion across the adjacent alpine meadow would weaken the regional carbon fixation capacity.

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