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Seasonal and interannual variations of ecosystem photosynthetic features in an alpine dwarf shrubland on the Qinghai-Tibetan Plateau, China

H.Q. LI[#,*,**], F.W. ZHANG[#,*,**], Y.N. LI[+,*,**], G.M. CAO[*,**], L. ZHAO[*,**], and X.Q. ZHAO[*,**]

Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, Qinghai 810001, China[*]
Key Laboratory of Adaptation and Evolution of Plateau Biota, Chinese Academy of Sciences, Xining, Qinghai 810001, China[**]

Abstract

Ecosystem photosynthetic characteristics are of utmost importance for the estimation of regional carbon budget, but such characteristics are not well understood in alpine regions. We collected CO_2 flux data measured by eddy covariance technique over an alpine dwarf shrubland on the Qinghai-Tibetan Plateau during years 2003–2010; and we quantified the temporal patterns of ecosystem apparent quantum yield (a), saturated photosynthetic rate (P_{max}), and ecosystem dark respiration (R_{De}). Results showed that the strong seasonality of a and R_{De} was driven mainly by air temperature (T_a), whereas that of P_{max} was much more determined by leaf area index rather than abiotic factors. Diurnal thermal fluctuation inhibited significantly the daytime photosynthetic capacity. Stepwise regression revealed that the seasonal deviations of a, P_{max}, and R_{De} were significantly controlled by T_a. The annual a was regulated mainly by annual growing season T_a, which indicated that the response of ecosystem a was instant. The annual variations of P_{max} correlated positively with soil temperature 5 cm below ground (T_s) of the annual nongrowing season and those of R_{De} related negatively with the annual nongrowing season precipitation. We suggested that a lagged response regulated the annual P_{max} and the annual R_{De}. Annual deviations of a and R_{De} were both significantly controlled by annual T_s, and those of P_{max} were marginally determined by annual PPFD. Thus, the future warming scenario, especially significant for nongrowing seasonal warming in the Qinghai-Tibetan Plateau, would favor ecosystem photosynthetic capacity in the alpine dwarf shrubland.

Additional key words: ecosystem photosynthetic parameters; eddy covariance technique; leaf area index; phenology; rectangular hyperbolic light response.

Introduction

Alpine terrestrial ecosystems store approximately 1,850 Pg (1 Pg = 10^{15} g) C and have important functions in the global C cycle; these functions are more prominent due to contemporary climate change (McGuire *et al.* 2009, Wookey *et al.* 2009). Shrub expansion is associated with climate warming in alpine grasslands and has become increasingly common (Chapin *et al.* 1995, Cannone *et al.* 2007, Vick and Young 2009). Such an expansion resulted in changes of C sink/source capacity over alpine regions (Oechel *et al.* 1993, Knapp *et al.* 2008, Yashiro *et al.* 2010). On one hand, shrubs sequester considerably more C, thereby possessing a higher C/N ratio in woody branches than grasses. On the other hand, soil organic matter and litter decompose, and C is released more rapidly under ongoing warming scenarios (Chapin *et al.* 1995, Sturm *et al.* 2005). However, insufficient information does not permit an accurate prediction of the alpine ecosystem C budget caused by shrub expansion. Compared to relative stable function of ecosystem respiration (Matthews *et al.* 2007), a, P_{max}, and R_{De} are indispensable

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[+]Corresponding author: fax: +86-971-6133353, phone: +86-971-6133353, e-mail: ynli@nwipb.cas.cn

Abbreviations: a – ecosystem apparent quantum yield; ADT – amplitude of diurnal temperature; EVI – enhanced vegetation index; LAI – leaf area index; NEE – net ecosystem CO_2 exchange; P_{max} – saturated photosynthesis rate; Q_{10} –the magnitude of respiration rate change for a change in temperature of 10°C; R_{De} – ecosystem dark respiration; SWC – volumetric water content of the soil 10 cm below ground; T_a – air temperature; T_c – shrub canopy temperature; T_s – temperature 5 cm below ground; VPD – vapour pressure deficit.

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photosynthetic parameters for couple C-climate models, which faithfully describe regional C dynamics (Cannell and Thornley 1998, Rastetter *et al.* 2003). Moreover, the C process in the alpine terrestrial ecosystem is much more controlled by the CO_2 uptake from photosynthesis than by the loss due to heterotrophic respiration (McFadden *et al.* 2003). The photosynthetic parameters are highly important in estimation of the alpine C budget. Furthermore, broad temperature regimes in alpine regions indicate the strong ability of native species for photosynthetic acclimation to temperature (Niu *et al.* 2008, Xiong *et al.* 2000).

Many recent studies derived mostly ecosystem a, P_{max}, and R_{De} from the rectangular hyperbolic function between the daytime net ecosystem CO_2 exchange (NEE) and PPFD with the eddy covariance technique (Falge *et al.* 2001, McFadden *et al.* 2003, Zhang *et al.* 2006, Wohlfahrt *et al.* 2008). Studies have been focused on the following related aspects of these important parameters: the intra- and inter-seasonal variations, and their response to phenology (McFadden *et al.* 2003), abiotic factors [soil water status, temperature, and vapour pressure deficit (VPD)] (Flanagan *et al.* 2002, Fu *et al.* 2006), and grazing management (Wohlfahrt *et al.* 2008, Redondo-Gómez *et al.* 2010). However, most of these studies focused only on low-lying grasslands (Gilmanov *et al.* 2003, 2007). Alpine vegetation is subjected to various ecosystem-specific conditions, including harsh climate (*e.g.*, huge diurnal thermal fluctuations, strong wind, and intense solar radiation), and low CO_2 concentrations; thus, the photosynthetic characteristics are expected to be much more different than those on plain ecosystems (Xu *et al.* 2006).

The Qinghai-Tibetan Plateau covers an area of 2.5×10^6 km^2 in western China, and it has an important function in the Asian C cycle and climate change. The alpine shrubland is one of the dominant vegetation types and covers 4.2% of the plateau (Zheng *et al.* 2000). It absorbs approximately 67.0 g (C) m^{-2} year^{-1} but with great annual variations (Zhao *et al.* 2006). Thus, long-term patterns of photosynthetic characteristics at the ecosystem level are particularly important in parameterizing the C-cycle model, but it has not been yet fully understood within the alpine region (Kato *et al.* 2004, Xu *et al.* 2006, Zhao *et al.* 2006). In this study, we analyzed the seasonal and interannual variations in a, P_{max}, and R_{De}. We quantified the potential environmental variables accounting for those temporal variations over the alpine dwarf shrubs to improve our understanding of parameterization for the C- cycle model. Given that the alpine shrubland ecosystem was nutrient-limited (Körner 1999) and had good snow-holding capacity (Starr *et al.* 2008), we hypothesized that temperature, rather than water conditions, had the predominant function in the temporal patterns of photosynthetic parameters.

Materials and methods

Site description: The flux tower was established in 2002 and is located in the northeastern region of the Qinghai-Tibetan Plateau (37°40′N, 101°20′E; 3,400 m a.s.l.). It is positioned about 5 km north of the Haibei Alpine Meadow Ecosystem Research Station, Chinese Academy of Sciences (Haibei Station, CAS). The area has a mean annual T_a of –1.70°C and yearly precipitation amount of 570 mm, 80% of which falls from May to September. The alpine shrub is a representative type of vegetation, and the vegetation structure has a two-layer canopy. The upper canopy is dominated by deciduous, dwarf shrub (*Potentilla fruticosa*), which is about 40–60 cm high and its relative vegetation coverage is about 60–80%. The lower canopy is occupied by C_3 grasses, mainly *Stipa aliena*, *Elymus nutans*, *Aster flaccidus*, and *Saussurea nigrescens*. The soil is classified as Mol-Cryic Cambisols; it is rich in soil organic matter but poor in available nitrogen. The study area is flat, homogeneous and about 12 km^2; yaks and Tibetan sheep graze on the vegetation in the winter in a low rate of about 1 yak ha^{-1}. Similar to other studies (Fu *et al.* 2006, Zhao *et al.* 2006), the growing season lasts from April 20 to October 15 and the nongrowing season is from October 16 to April 19.

Measurements: A three-dimensional sonic anemometer (*CSAT-3*, *Campbell Scientific Inc.*, UT, USA) and infrared open-path CO_2/H_2O analyzer (*LI-7500*, *LI-Cor Inc.*, NE, USA) were positioned at 2.2 m above the ground. Raw data were sampled at 10 Hz, and included the following: 3D wind speed, sonic virtual temperature, and CO_2 and H_2O concentrations. The mean, variance, and covariance of these data were calculated and logged every 30 min using a *CR5000* (*Campbell Scientific Inc.*, UT, USA). The CO_2/H_2O analyzer system was calibrated in April each year.

T_a and relative humidity were monitored by a temperature and humidity probe (*HMP45C*, *Vaisala*, Finland). Wind speed and direction were determined by a cup anemometer and dogvane (*034A-L* and *014A*, *RM Young*, MI, USA), respectively. All meteorological factors were measured at the same heights of 1.5 and 2.5 m. Shrub canopy temperature (T_c) was measured by an infrared thermocouple sensor (*IRTS-P*, *Apogee Instruments Inc.*, Logan, UT, USA) situated 1.5 m above ground. Radiation and PPFD were monitored by four radiometers (*CM11*, *Kipp & Zonen*, Netherlands) and a quantum sensor (*LI-190SB*, *Li-Cor*, Nebraska, USA), respectively, each positioned at 1.5 m above ground. Precipitation was collected by a rain gauge (*52203*, *RM Young*, MI, USA) that was positioned 0.5 m above ground. Using a thermocouple probe (*105T*, *Campbell Scientific Inc.*, UT, USA), soil temperature (T_s) was measured at five layers: 0.05, 0.1, 0.2, 0.4, and 0.8 m below ground. Soil volumetric water content (SWC) was monitored by a time domain reflectometer (*CS616*, *Campbell Scientific Inc.*, UT, USA) at 2 different layers, *i.e.*, 0.1 and 0.2 m below ground. All routine variables were recorded at 30-min intervals and logged as 30-min averages in a data logger (*CR23X*, *Campbell Scientific Inc.*, UT, USA).

To survey the phenological features in a shrub ecosystem accurately, we used the leaf area index (LAI) and the enhanced vegetation index (EVI) data from 8 d composite LAI (MOD15A2) and 16 d vegetation indices (MOD13Q1), respectively. The spatial resolution was 1 km × 1 km. LAI and EVI were obtained from the *MODIS* land product subsets and Oak Ridge National Laboratory Distributed Active Archive Center (http://daac.ornl.gov/MODIS/modis.html). Monthly EVI and LAI were averaged for the following analyses. Although LAI and EVI were not zero, which was fairly unreasonable during nongrowing season, we used this value for data integrity. This technique for estimating shrubland phenology compared very favorably (r^2=0.73, n = 10, p<0.05) with the harvesting methods (Wohlfahrt *et al.* 2008) for green LAI (unpublished data from 2005 to 2007).

Data processing: Missing microclimate data (excluding radiation) were interpolated, and the gap-filling strategy was performed as follows: (*1*) the simple linear method was performed for the data gaps less than half day length (<24 h); (*2*) on condition that the data gaps were beyond half day length, we assumed that the occurrence of the maximum and minimum were fixed (*e.g.*, the daily maximum and minimum T_a occurred at 14:00 and 05:00 of Beijing standard time, respectively). Thus, first we performed the spline method for interpolating the maximum and/or minimum of the gap with the daily maximum and/or minimum of 5 d before and after this gap. Then, we filled the remaining gaps linearly. Radiation data were the function of time, elevation, location, and atmospheric condition. We parameterized the function and interpolated missing radiation data.

Flux data were subjected to *Webb-Pearman-Leuning* corrections because of vapour fluctuation (Webb *et al.* 1980). Daytime was defined as the time when global radiation exceeded 1 W m^{-2} and PPFD exceeded 10 μmol (photon) m^{-2} s^{-1}. The daytime NEE was removed when precipitation emerged or when the absolute value of NEE was above 1.0 mg(CO$_2$) m^{-2} s^{-1}. Meanwhile, the growing season NEE was assumed to be normally distributed and rejected by the filter: $|x - \bar{x}| > 3\ \delta$ ($\bar{x}$ and δ are the mean value and SD) at the 5 d moving windows. The a, $P_{\max}$, and R_{De} were estimated using the following rectangular hyperbolic Michaelis–Menten equation (Eq. 1) (Falge *et al.* 2001, Serrano-Ortiz *et al.* 2007, Zhang *et al.* 2006):

$$\mathrm{NEE} = R_{\mathrm{De}} - \frac{a \times P_{\max} \times \mathrm{PPFD}}{a \times \mathrm{PPFD} + P_{\max}} \qquad (1)$$

The growing season data were fitted with the equation with the 120 valid data (about 5 d) windows. The response parameters were estimated in *Matlab 7.4* (*Mathworks Inc.*, MA, USA), and the results were kept if significant at p<0.05 and determinant coefficient of r^2>0.20. The abiotic factors were calculated by the average or sum (for precipitation) principle at the corresponding fitting windows. With the exception of power failure for the entire month in September 2005, available data for the other seven years were approximately 82% of daytime records.

Results

Environmental factors and plant growth: The monthly variations in all variables demonstrated remarkable seasonal patterns (Fig. 1). Annual T_a was –1.42°C ranging from –0.65°C in 2009 to –1.87°C in 2004. T_c showed a pattern similar to T_a; the mean annual value was 1.14°C. Growing season VPD and SWC were 0.32 kPa and 0.28 cm^3 cm^{-3}, respectively.

Annual PPFD was 313.27 μmol(photon) m^{-2} s^{-1}; it showed significant interannual fluctuations, with a maximum of 364.79 in 2003 and a minimum of 273.64 in 2010. The e-year average precipitation amount was 459.8 mm; 95.4% was concentrated into the growing season. During the growing season, climatic conditions were favorable for plant growth, and the average maximum LAI was up to 2.2 at the end of July (Fig. 1*D*). Annual LAI and EVI were 0.66 and 0.40, respectively, and the annual maxima were 0.71 and 0.45 (both in 2007), respectively. No significant correlation was observed between annual T_a and annual T_s during the nongrowing period (p=0.63), which was mainly induced by snow trapped in shrubland.

Seasonal and interannual variations in *a*: The 8-year average of a was 0.0011 mg(CO$_2$) μmol^{-1}(photon), and it ranged from 0.0008 mg(CO$_2$) μmol^{-1}(photon) in 2008 to 0.0014 mg(CO$_2$) μmol^{-1}(photon) in 2010. The average peak value was 0.0019 mg(CO$_2$) μmol^{-1}(photon), and it appeared at the end of July or at the beginning of August (Fig. 2*A*); this peak coincided with the seasonal peak patterns of temperature, LAI, and EVI (Fig. 1*D*). Stepwise linear regression with abiotic factors showed that seasonal variations in a were largely controlled by T_a (Table 1), and it could be described by the Arrhenius equation (Eq. 2).

$$a = 0.0044 e^{\frac{117596.05}{8.134}\left(\frac{1}{288.16} - \frac{1}{T_a + 273.16}\right)}$$
$$(r^2 = 0.78,\ n = 49,\ p < 0.001) \qquad (2)$$

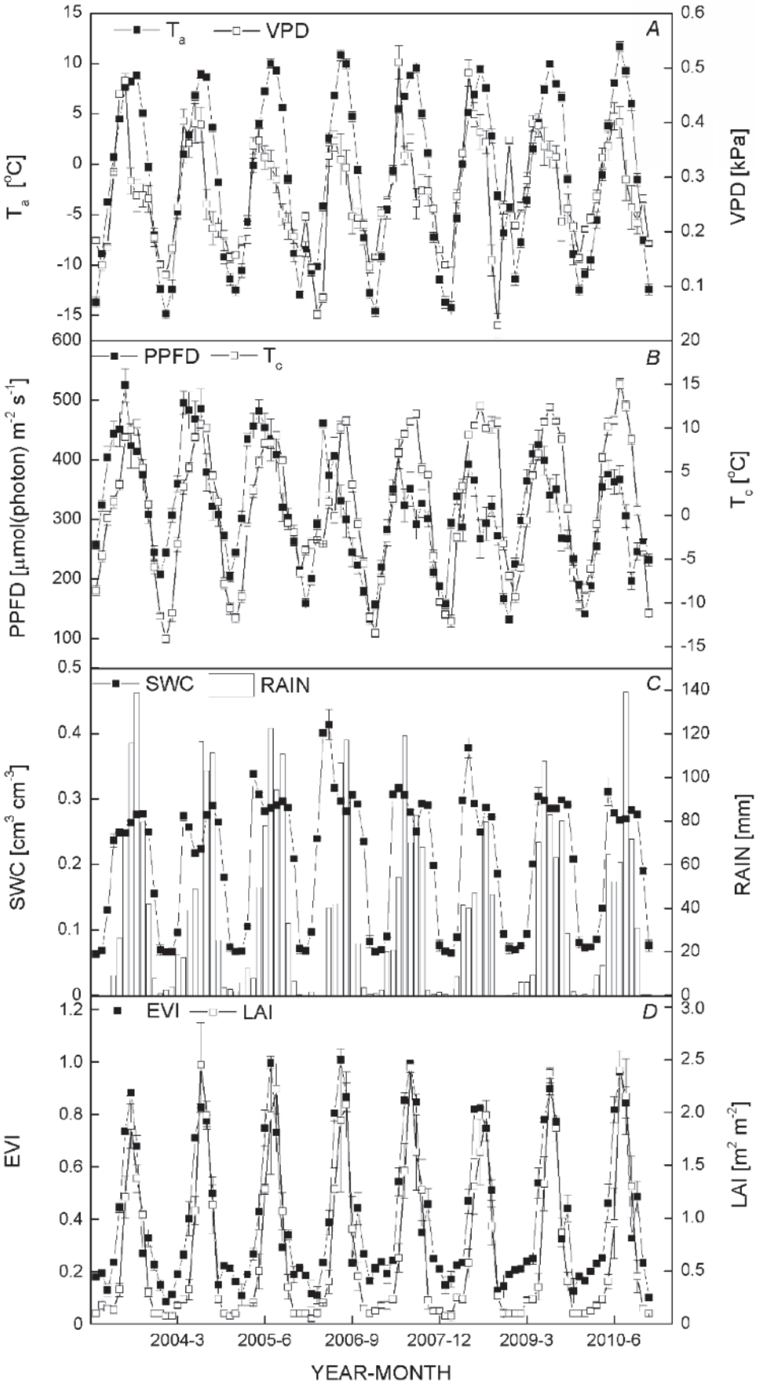

Fig. 1. Intra- and interseasonal variations in abiotic and biotic factors (air temperature (T_a) and vapour pressure deficit (VPD), PPFD, and shrub canopy temperature (T_c), soil water content (SWC) at 10 cm and rainfall (RAIN), enhanced vegetation indexes (EVI), and leaf area indexes (LAI).

Eq. 2 showed that alpine shrub ecosystem *a* could reach 0.0044 mg(CO_2) μmol(photon)$^{-1}$, whereas T_a could reach 15ºC barring other limitations. LAI, rather than EVI, accounted for more seasonal variations in *a* (Table 1). T_a exerted a positive exponential influence on LAI ($LAI = 0.38\ e^{0.17\times T_a}$, $r^2 = 0.81$, $p<0.001$). Moreover, the general linear model of *a* with T_a and LAI showed the main effect of LAI was not significant. Furthermore, the seasonal deviation (defined as the standard deviation of corresponding data) of *a* was also controlled by T_a (Fig. 3*A*). Thus, T_a had a predominant function in the seasonal fluctuations in the ecosystem *a*, including its effect on LAI. At an interannual scale, the stepwise regression results revealed that T_a, more specifically, the annual growing season T_a (r^2=0.71, p=0.005), was the dominant factor in the interannual changes in *a* (Table 2). The annual deviation of *a* was controlled by annual T_s (Fig. 4*A*).

Table 1. Linear regressions between the monthly photosynthetic parameters and monthly climatic and biotic factors, including the mean air temperature (T_a), PPFD, soil temperature (T_s) at 5 cm, volumetric soil water content (SWC) at 10 cm, rainfall amount (RAIN), vapour pressure deficit (VPD), enhanced vegetation indexes (EVI) and leaf area indexes (LAI).

Factor	a [mg(CO$_2$) μmol(photon)$^{-1}$]			P_{max} [mg(CO$_2$) m^{-2} s^{-1}]			R_{De} [mg(CO$_2$) m^{-2} s^{-1}]		
	Linear equation	r^2	p	Linear equation	r^2	p	Linear equation	r^2	p
T_a (x_1)[°C]	$y = 0.00015\ x_1 + 0.00011$	0.75	<0.001	$y = 0.074\ x_1 + 0.062$	0.74	<0.001	$y = 0.0091\ x_1 + 0.040$	0.62	<0.001
PPFD (x_2) [μmol(photon) m^{-2} s^{-1}]	$y = 2.31E\text{-}07\ x_2 + 0.00086$	0.01	0.86	$y = -0.00025\ x_2 + 0.56$	0.01	0.68	$y = 2.08E\text{-}05\ x_2 + 0.082$	0.01	0.81
T_s (x_3) [°C]	$y = 0.00015\ x_3 - 0.00011$	0.67	<0.001	$y = 0.080\ x_3 - 0.21$	0.74	<0.001	$y = 0.0091\ x_3 + 0.012$	0.58	<0.001
SWC (x_4)[cm^3 cm^{-3}]	$y = 0.00051\ x_4 + 0.00080$	0.01	0.83	$y = -0.36\ x_4 + 0.56$	0.01	0.76	$y = 0.13\ x_4 + 0.054$	0.02	0.41
RAIN (x_5)[RAIN]	$y = 1.25E\text{-}05\ x_5 + 9.66E\text{-}05$	0.42	<0.001	$y = 0.0063\ x_5 + 0.039$	0.45	<0.001	$y = 0.00071\ x_5 + 0.042$	0.31	<0.001
VPD (x_6) [kPa]	$y = 0.0018\ x_6 + 0.00035$	0.03	0.12	$y = 0.80\ x_6 + 0.20$	0.02	0.15	$y = 0.15\ x_6 + 0.40$	0.07	0.041
EVI (x_7)	$y = 0.0020\ x_7 - 0.00027$	0.60	<0.001	$y = 1.06\ x_7 + 0.062$	0.68	<0.001	$y = 0.13\ x_7 + 0.012$	0.58	<0.001
LAI (x_8) [m^2 m^{-2}]	$y = 0.00076\ x_8 + 6.89E\text{-}05$	0.66	<0.001	$y = 0.43\ x_8 - 0.032$	0.90	<0.001	$y = 0.049\ x_8 + 0.034$	0.62	<0.001

Table 2. Linear regressions between the annual photosynthesis parameters and annual climatic and biotic factors, including the mean air temperature (T_a), PPFD, soil temperature (T_s) at 5 cm, volumetric soil water content (SWC) at 10 cm, rainfall amount (RAIN), vapour pressure deficit (VPD), enhanced vegetation indexes (EVI) and leaf area indexes (LAI).

Factor	a [mg (CO$_2$) μmol(photon)$^{-1}$]			P_{max} [mg(CO$_2$) m^{-2} s^{-1}]			R_{De} [mg(CO$_2$) m^{-2} s^{-1}]		
	Linear equation	r^2	p	Linear equation	r^2	p	Linear equation	r^2	p
T_a (x_1)[°C]	$y = 0.00036\ x_1 + 0.0015$	0.50	0.03	$y = 0.051\ x_1 + 0.62$	0.01	0.58	$y = 0.015\ x_1 + 0.12$	0.16	0.18
PPFD (x_2) [μmol(photon) m^{-2} s^{-1}]	$y = -1.07E\text{-}06\ x_2 + 0.0014$	0.01	0.59	$y = -0.0016\ x_2 + 1.05$	0.45	0.04	$y = -0.00022\ x_2 + 0.17$	0.59	0.02
T_s (x_3) [°C]	$y = 0.00016\ x_3 + 0.00067$	0.07	0.26	$y = 0.078\ x_3 + 0.34$	0.11	0.22	$y = 0.012\ x_3 + 0.069$	0.23	0.13
SWC (x_4)[cm^3 cm^{-3}]	$y = 0.00085\ x_4 + 0.00093$	0.01	0.84	$y = 1.23\ x_4 + 0.30$	0.01	0.50	$y = 0.31\ x_4 + 0.038$	0.19	0.16
RAIN (x_5)[RAIN]	$y = 8.90E\text{-}07\ x_5 + 0.00070$	0.01	0.50	$y = -0.00055\ x_5 + 0.81$	0.01	0.34	$y = -8.53E\text{-}05\ x_5 + 0.14$	0.08	0.25
VPD (x_6) [kPa]	$y = 0.0020\ x_6 + 0.00055$	0.01	0.60	$y = 0.51\ x_6 + 0.42$	0.00	0.77	$y = -0.012\ x_6 + 0.11$	0.00	0.96
EVI (x_7)	$y = 0.0048\ x_7 - 0.00080$	0.33	0.08	$y = 2.21\ x_7 - 0.33$	0.34	0.07	$y = 0.30\ x_7 - 0.019$	0.42	0.05
LAI (x_8) [m^2 m^{-2}]	$y = 0.0017\ x_8 - 2.74E\text{-}05$	0.02	0.33	$y = 1.24\ x_8 - 0.26$	0.30	0.09	$y = 0.069\ x_8 + 0.057$	0.00	0.51

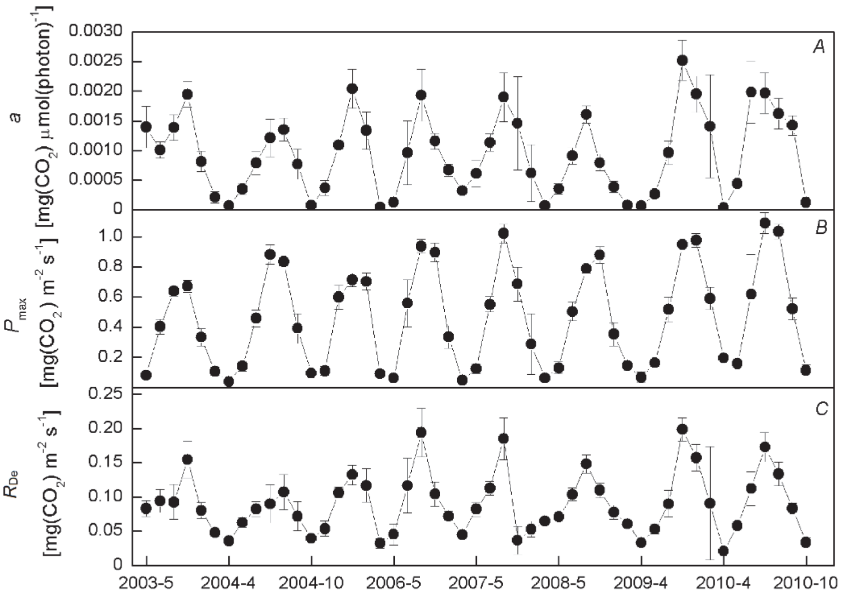

Fig. 2. Intra- and interseasonal patterns of ecosystem apparent quantum yield (*a*), saturated photosynthesis rate (P_{max}), and ecosystem dark respiration (R_{De}).

Seasonal and inter-annual variations in P_{max}: P_{max} showed distinct, unimodal, seasonal variations, and its maximum was also observed in July or in August (Fig. 2*B*). Stepwise regression showed that T_s (T_a) was the most important abiotic factor (Table 1). Further analysis revealed that the exponential relationship was more apparent for temperature and P_{max}, with considerably greater explanatory power from T_s ($r^2 = 0.82$, $p<0.001$). However, P_{max} better correlated with LAI, showing a positive linear correlation (Table 1). Furthermore, a significant relationship was observed between LAI and residual from P_{max} and T_s ($|P_{max}\ (\text{residual})| = 0.054 \times \text{LAI} + 0.054$, $r^2 = 0.22$, $p<0.001$). This relationship suggests that LAI, rather than T_s, had an important function in the seasonal variations in P_{max}. The seasonal deviation of P_{max} was significantly albeit weakly controlled by T_a (Fig. 3*B*). At the interannual scale, the annual P_{max} ranged from 0.72 (in 2010) to 0.44 mg(CO_2) m^{-2} s^{-1} (in 2003). The annual PPFD was the significant determining factor for annual variations in P_{max}, which might be a statistical coincidence (Table 2). The relationship between annual P_{max} and the nongrowing season T_s could be better described by an exponential equation ($r^2 = 0.60, p=0.026$).

Seasonal and interannual variations in R_{De}: Seasonal R_{De} exponentially correlated with T_a, and it could be also described by the Van't Hoff equation (Eq. 3).

$$R_{De} = 0.26\ e^{\ln 3.43(T_a - 15)/10}$$
$$(r^2=0.68, n = 49, p<0.001) \qquad (3)$$

Eq. 3 showed that the magnitude of respiration rate change for a change in temperature of 10°C (Q_{10}) of the daytime R_{De} was 3.43 during the growing season. Average peak R_{De} was 0.16 mg(CO_2) m^{-2} s^{-1}, which occurred simultaneously with that of *a* in July or in August (Fig. 2*C*). LAI explained 62.1% of the seasonal variability of R_{De}, having slightly lesser explanatory power than that of T_a. However, the general linear model showed that the main effect of LAI had no significant influence on R_{De}. The seasonal deviation of R_{De} was significantly controlled by T_a (Fig. 3*C*). Thus, T_a had a fundamental function in the seasonal variations in R_{De}. At the interannual scale, the 8-year mean value of R_{De} was 0.090 mg(CO_2) m^{-2} s^{-1}, ranging from 0.070 (in 2006) to 0.11 (in 2004). Annual PPFD exerted a significant influence on the variability of R_{De} (Table 2), but further analysis showed that annual R_{De} was much more negatively determined by the nongrowing season precipitation ($r^2=0.63$, $p=0.012$). The deviation of the annual R_{De} was significantly determined by annual T_s (Fig. 4*C*).

Discussion

Temperature and water availability effects: In the alpine shrub ecosystem, the seasonal and interannual variations in *a* were mostly controlled by T_a (Tables 1, 2). In the absence of C_4 plants in this area confirmed by Li *et al.* (2006), the quantum yield in C_3 species was temperature-dependent (Ehleringer and Pearcy 1983). It denied partially that the photosynthetic features of upland vegetation were alpine-specific (Xu *et al.* 2006). T_a was significantly and exponentially correlated with seasonal P_{max} and R_{De}, thereby indicating that the photosynthetic parameters were exponentially related to temperature. This result was ascribed to the following two reasons: (*1*) soil and plant enzymatic reaction rates increased exponentially with rising temperature (Wohlfahrt *et al.* 2008); (*2*) LAI, as the indicator of vegetation photosynthesis, was correlated also exponentially with temperature.

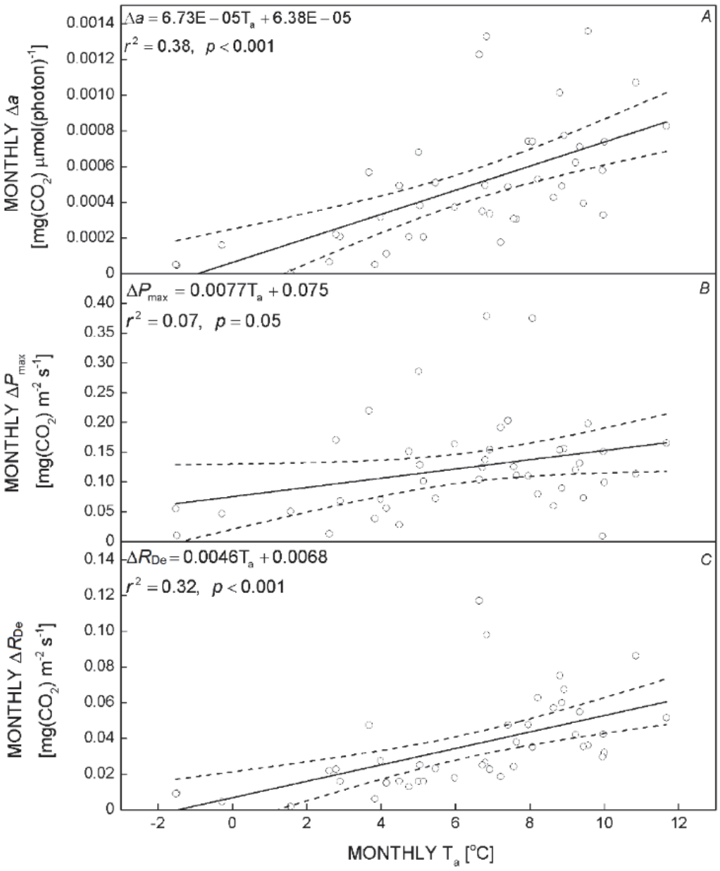

Fig. 3. Regressions between monthly standard deviation of photosynthetic parameters (Δa, $\Delta P_{\max}$, and $\Delta\ R_{\mathrm{De}}$) and monthly air temperature (T_a) (dashed line represented the 95% confidence).

If T_a reached 15ºC and no other limitations occurred, a and $P_{\max}$ would increase to values that were about 4- and 5 times higher than the current growing season values. Moreover, R_{De} would be double of the corresponding growing season value. This result indicated that the daytime C sequestration capacity was enhanced in a warming scenario, which was consistent with the observations of daytime gross production improvement in a warming experiment of an alpine dwarf shrub (Biasi *et al.* 2008). However, this result did not imply that the alpine shrub ecosystem C fixation potential was enhanced because of a corresponding increase in nocturnal respiration and soil organic matter and litter decomposition during the nongrowing season (Chapin *et al.* 1995, Wookey *et al.* 2009). Moreover, Q_{10} was approximately 4.5, which was slightly lower than that of a and $P_{\max}$. The nongrowing season ecosystem respiration was about two-thirds of the growing season CO_2 exchange (Zhao *et al.* 2006), and the ecosystem respiration may surpass the photosynthetic capacity in warmer conditions (McGuire *et al.* 2009). In conclusion, the daytime photosynthetic capacity was enhanced, whereas the ecosystem C sequestration potential might decrease in a warming scenario over the alpine dwarf shrub (Kato *et al.* 2006, Fu *et al.* 2009, Saito *et al.* 2009).

Some studies hypothesized that amplitude of diurnal temperature (ADT, defined as the difference of daytime and nocturnal air temperature) favors alpine C sequestration (Gu *et al.* 2005, Zhao *et al.* 2006). We found negative linear relationships between monthly photosynthetic characteristics and ADT ($r^2>0.11$, $p<0.01$). Moreover, the slope of $P_{\max}$ (–0.17) was much lesser than that of R_{De} (–0.018). It suggested that much greater ADT inhibited the daytime vegetation photosynthetic capacity and partially denied the aforementioned hypothesis at seasonal level. The potential reason might be less respiratory substrate was consumed by lower nocturnal ecosystem respiration, which originated mainly from photosynthetic products in alpine ecosystem (Fu *et al.* 2006, 2009). More substrate conservation would limit the daytime photosynthesis activity.

Photosynthetic traits are related to water stress at the leaf and ecosystem levels (Fu *et al.* 2009, Ruimy *et al.* 1995, Zhang *et al.* 2006). Although stomata have been shown to respond sensitively to VPD, stomatal conductance exerts a minimal influence on photosynthesis in alpine plants unless VPD exceeds 1.5 kPa, which rarely occurs in alpine regions (Körner 1999). The fact that VPD did not inhibit photosynthetic process at out study site was also reflected in the statistically insignificant correlation between VPD and photosynthetic parameters. Even during flourishing growth (from July to August), only $P_{\max}$ was marginally significantly correlated with VPD ($P_{\max} = 1.09 \times \mathrm{VPD} + 0.50$, $r^2=0.26$, $n = 12$, $p=0.054$).

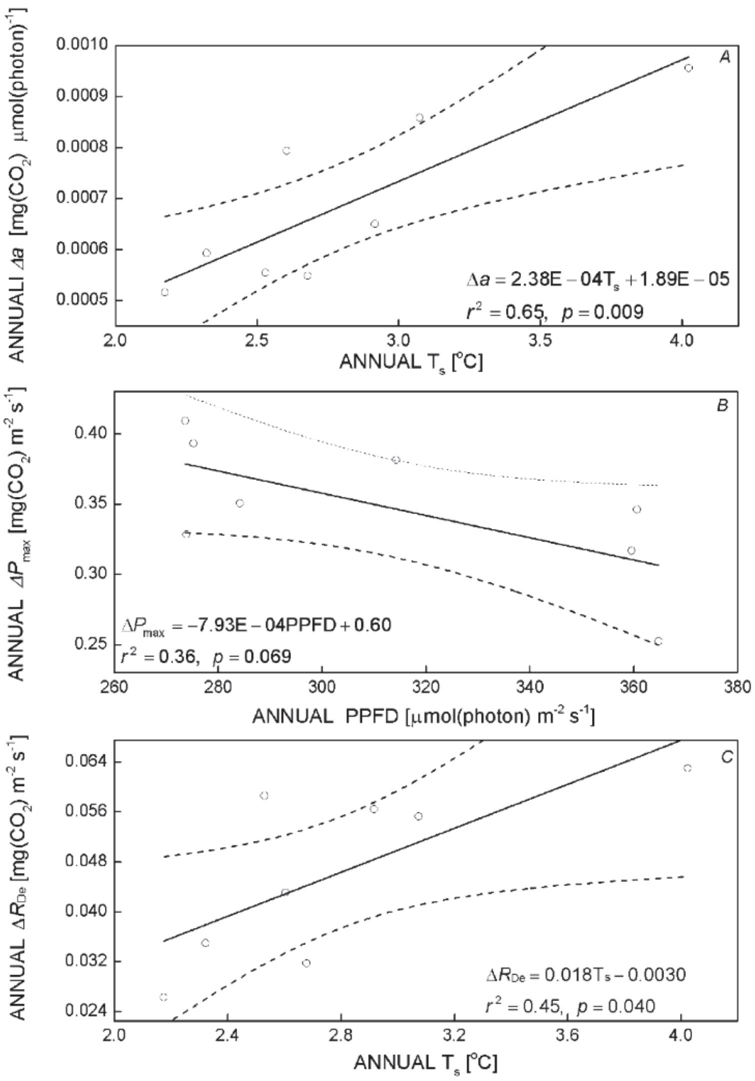

Fig. 4. Regressions between annual standard deviation of photosynthetic parameters (Δa, ΔP_{max}, and ΔR_{De}) and climatic factors (annual 5 cm soil temperature (T_s) and annual PPFD) (*dashed line* represented the 95% confidence).

Two possible specific explanations could describe this relationship: (*1*) shrubs have deep roots and a good snow-holding capacity; thus, shrub ecosystems have abundant water supply in the early growing season because of snow melting (Strack *et al.* 2007, Sturm *et al*. 2005); (*2*) more than 87% of precipitation is concentrated in the growing season, and the summer drought rarely occurred in this area (Gu *et al.* 2003). Additionally, SWC had a minimal influence on the ecosystem photosynthetic characteristics (Fu *et al*. 2006, 2009). In brief, the current water status had a negligible function in patterns of photosynthetic parameters in the alpine shrubland ecosystem. The insensitivity to water availability might be a critical factor for shrub expansion in future, significantly warmer and drier scenarios in the Qinghai-Tibetan Plateau.

Interestingly, T_s and precipitation of the nongrowing season had important functions in the annual variations in P_{max} and R_{De}, thereby confirming a lagged response of these parameters to the nongrowing season conditions (Marcolla *et al.* 2011). Together with the response of annual variations in *a* to the growing season temperature (Table 2), the results indicated that *a* was an instant variable, whereas P_{max} and R_{De} were compound photosynthetic parameters. The alpine ecosystem is nutrient-limited, and plant photosynthetic activity is inhibited by available nitrogen. Higher T_s during the nongrowing season stimulated higher litter decomposition and faster nutrient mineralization (Hobbie and Chapin 1996), which could increase the available nutrient supply and favor plant growth. This was the potential reason why lagged response occurred. Moreover, nongrowing seasonal warming was significant and considerably greater in the Qinghai-Tibetan Plateau (Zhang *et al.* 2013), suggesting that P_{max} would be enhanced.

Magnitude of phenology influence: LAI and EVI illustrated the important influence on intra- and interannual patterns of P_{max} (Tables 1, 2), which agreed very well with the observation that ecosystem C uptake potential was driven more by the assimilating plant area than by other biotic and (or) abiotic variables (Vourlitis and Oechel 1999, Wohlfahrt *et al*. 2008). This result confirmed the minimal trade-off between the increasing assimilating

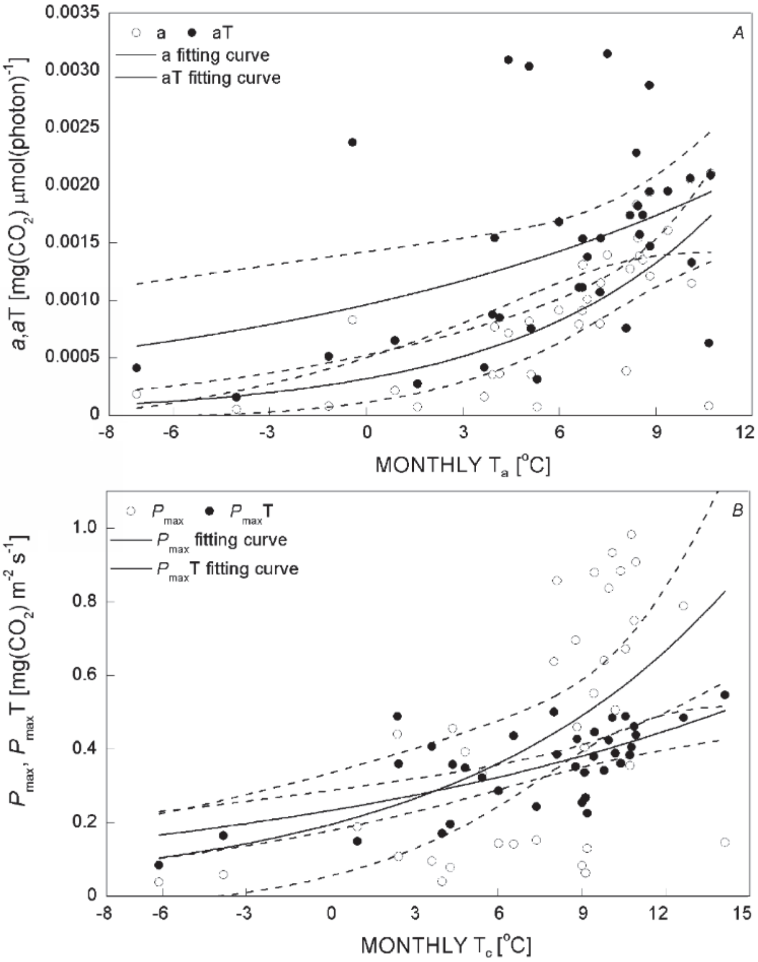

Fig. 5. Relative contribution of T_a (T_c) to alpine dwarf shrubland ecosystem *a* and P_{max}. *a* T and P_{max} T were *a* and P_{max} normalized with corresponding EVI and LAI, respectively. The above fitting curve suggested that its effect on *a* and P_{max} was greater (*dashed line* represented the 95% confidence).

plant area and self-shading until LAI reaches 4.0 m^2 m^{-2} in alpine shrubland (McFadden *et al.* 2003, Wohlfahrt *et al.* 2008) and slightly different species-specific photosynthetic capacity (Starr *et al.* 2008). The high correlation was found between monthly P_{max} and R_{De} (r^2=0.71, p<0.01), and this was probably due to the fact that plant maintenance and soil microbial respiration depend on available substrate mainly supplied by photosynthetic activity (Fu *et al.* 2009, McFadden *et al.* 2003).

LAI and EVI were highly sensitive to grazing management in the alpine region. The timing and frequency of pasture management are crucial to understand and/or manage alpine ecosystem C sequerstration (Wohlfahrt *et al.* 2008), particularly, in the state of grassland degradation caused by heavy grazing rather than by warming in an alpine ecosystem (Wang *et al.* 2012).

To distinguish the respective effects between temperature and EVI (LAI) on the ecosystem photosynthetic characteristics, a simple normalized method was performed (Zhang *et al.* 2006). EVI and LAI were the predominant biotic determinants of seasonal variations in *a* and P_{max}, respectively (Table 1). *a*T and P_{max}T was the ecosystem *a* and P_{max} normalized by the corresponding EVI and LAI, which indicated the effects of temperature on ecosystem photosynthesis with background EVI and LAI (Fig. 5).The difference between *a* and *a*T (P_{max} and P_{max}T) represented the contribution of increased EVI (LAI) from vegetation development to ecosystem photosynthetic characteristics during the growing season. The difference between *a* and *a*T was negative (Fig. 5*A*), which suggests that T_a could impose a more important effect on *a* than EVI. This result coincided with the observation that *a* is slightly influenced by flora growth status (Field and Mooney 1983). Nevertheless, the relationship between P_{max} and P_{max}T was slightly different. T_c could more influence P_{max} than LAI when T_c was below 4.1 °C (Fig. 5*B*, corresponding T_a was 3.0 °C in May). Along with the increase in T_c, LAI became a markedly more important determinant of seasonal variations in P_{max}. Thus, biotic factors had a much more important function during the middle of the growing season. Much stronger effect of LAI and lesser influence of T_c confirmed also that P_{max} of alpine vegetation was a little species-specific and had good capacity of acclimation to temperature (Xiong *et al.* 2000).

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