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Seasonal variations of ecosystem apparent quantum yield (α) and maximum photosynthesis rate ($P_{\max}$) of different forest ecosystems in China

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Abstract

Continuous measurements of carbon dioxide using the eddy covariance (EC) technique were made in 2003 at three ChinaFLUX forest sites, including a temperate mixed forest (CBS), a subtropical evergreen coniferous plantation (QYZ) and a subtropical evergreen broad-leaved forest (DHS) along the North–South Transect of Eastern China (NSTEC). The three forest sites are influenced by Asian monsoon climate to varying degrees. The environmental controls on the seasonal variations of ecosystem apparent quantum yield (α), maximum photosynthesis rate ($P_{\max}$) and ecosystem respiration (R_e) were investigated in the three forest ecosystems. At the CBS site, temperature was found to be the dominant factor controlling the seasonal patterns of ecosystem α and $P_{\max}$, while the phenology, which was mainly embodied by the development of LAI, also displayed important influence. The seasonal patterns of α and $P_{\max}$ at QYZ were mainly ascribed to vapor pressure deficit (VPD). Ecosystem α decreased with increasing VPD and $P_{\max}$ decreased below and above the optimum VPD as a result of the Asian subtropical monsoon climate which resulted in the extremely high temperature and low moisture. At the DHS site, ecosystem α only appeared weak negative correlation with temperature, while there was no obvious dominant factor controlling the seasonal pattern of ecosystem $P_{\max}$. The ecosystem respiration of the three forest ecosystems could be estimated well by temperature with an exponential equation. During the growing season, the ecosystem α, $P_{\max}$ and R_e at CBS were much stronger than that of QYZ and DHS. The R_e at CBS was more sensitivity to temperature than that of QYZ and DHS, so its response to changing climate deserved more attention in the evaluation of the carbon budget of such ecosystem.

Keywords: Photosynthetic capacity; Drought; Monsoon climate; Eddy covariance

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1. Introduction

Forest ecosystems play an important role in global carbon balance due to their large carbon storage and exchange which are influenced by the changing climate and environment (Valentini et al., 2000; Barford et al.,

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2001). The quantum yield (α), photosynthetic capacity (P_{max}) and respiration (R_e) of forests have received worldwide attention in the evaluation of the global carbon budget (Ruimy et al., 1995). Photosynthesis has been extensively studied at leaf level, and numerous photosynthetic models have been developed (Farquhar et al., 1980; Ball et al., 1987; Collatz et al., 1992; Leuning, 1995; Tuzet et al., 2003; Yu et al., 2001, 2003). Recently, many studies have focused on the photosynthesis at ecosystem level with the eddy covariance (EC) technique (Griffis et al., 2003; Baldocchi, 2003).

The ecosystem α, P_{max} and R_e are important parameters for describing ecosystem photosynthetic activity and determine the shape of the light response curve (Schulze and Caldwell, 1994; Ruimy et al., 1995), which could be derived from the relationship between net ecosystem CO_2 exchange (N_{EE}) and photosynthetic photon flux density (e.g. Ruimy et al., 1995). The relationship is also often utilized in the gap filling of flux measurement (Falge et al., 2001; Griffis et al., 2003). The seasonal and inter-annual variations of ecosystem α and P_{max} (Wofsy et al., 1993; Hollinger et al., 1999; Griffis et al., 2003; Lee et al., 1999) and their responses to temperature (Hollinger et al., 1999), VPD (Loescher et al., 2003; Carrara et al., 2004) have been studied previously for a range of ecosystems. However, most studies have focused on boreal and temperate forests (Wofsy et al., 1993; Hollinger et al., 1999; Griffis et al., 2003; Lee et al., 1999; Loescher et al., 2003; Carrara et al., 2004), such studies are still insufficient on other forest ecosystems.

China is one of the largest countries in the Eurasian continent with a clear latitudinal pattern of forest types in eastern China, ranging from the coniferous forest in the north, deciduous broad-leaved forest, mixed forest, evergreen broad-leaved forest, tropical seasonal rainforest, and tropical rainforest in the south along the North–South Transect of Eastern China (NSTEC) (Yu et al., 2006). However, relatively few long-term studies of water vapour and carbon dioxide fluxes at ecosystem level have been made until now in China. ChinaFLUX has been established since late August in 2002, which applies the EC technique of microclimatology as a main research method to study fluxes of CO_2, water and heat between vegetation and the atmosphere (Yu et al., 2006). ChinaFLUX provides us with a special opportunity to study the ecosystem α, P_{max} and R_e on typical forest ecosystems in China. In this study, the seasonal patterns and environmental control of the ecosystem α, P_{max} and R_e were investigated in three ChinaFLUX forest sites including a temperate mixed forest (CBS), a subtropical evergreen coniferous plantation (QYZ) and a subtropical, evergreen broad-leaved forest (DHS), which will improve our understanding of the parameterization of carbon cycle models and the gap filling in flux measurement.

2. Methods and materials

2.1. Site description

In this study, we utilized data collected in 2003 from three ChinaFLUX sites: Changbaishan temperate broad-leaved Korean pine mixed forest (CBS), Qianyanzhou subtropical *Pinus* plantation (QYZ) and Dinghushan subtropical, evergreen broad-leaved forest (DHS). An overview of the site characteristics of CBS, QYZ and DHS sites is given in Table 1. More extensive description of the sites could be found in Yu et al. (2006), Wen et al. (2006) and Guan et al. (2006).

2.2. Measurements

The flux and routine meteorological measurements were operated with the same set of instruments and program within the three forest sites in ChinaFLUX (Yu et al., 2006). Table 1 describes the observation heights of different sensors. The fluxes of CO_2, H_2O and energy were measured with the eddy covariance (EC) technique at the three sites and recorded by a datalogger (Model CR5000, Campbell Scientific, Logan, UT, USA) at 30 min intervals. The EC system consists of a three-dimensinal sonic anemometer (model CSAT-3, Campbell Scientific Inc., Logan, UT, USA) and an infrared open-path H_2O/CO_2 analyzer (model LI-7500, Li-Cor Inc., Lincoln, NE, USA). The routine meteorological factors were also measured simultaneously and continuously along with the EC fluxes. Global radiation and photosynthetic photon flux density (Q_{PPFD}) were measured with a radiometer (CM11, Kipp & Zonnen, Delft, NL) and a quantum sensor (LI190SB, LICOR Inc.), respectively. The Q_{PPFD} under the canopy was measured with a quantum sensor (LQS7010-SUN, APOGEE, Logan, UT, USA). The air temperature and relative humidity profiles were measured with shielded and aspirated probes (HMP45C, Campbell Scientific Inc.) at seven heights above and within the canopy. Precipitation was recorded with a rain gauge (52203, Rm Young, Traverse City, MI, USA) at the top of the flux tower. Soil temperature was measured with thermocouple probe (105T, Campbell Scientific Inc.), and soil volumetric water content was measured with water content reflectometer (CS616, Campbell Scientific Inc.). All the meteorological measurements were

Table 1
Physical feature and measurement height of three forest study sites

Site[a]	CBS	QYZ	DHS
Location	41°29′N, 128°05′E	26°44′N, 115°04′E	23°10′N, 101°12′E
Topography	Flat terrain	Hilly region	Hilly region
Elevation (m)	736	100	300
Mean daytime air temperature (°C)[b]	6.2	19.6	21.1
Precipitation (mm)[c]	496.3	855	1289
Soil type	Dark brown soil	Red soil	Lateritic red soil yellow soil
Canopy height (m)	26	11	15
LAI ($m^2\ m^{-2}$)	5.0[d]	3.6	4.0
Dominant species	*Pinus koraiensis*, *Tilia amurensis*, *Quercus mongolica*, etc.	*Pinus elliottii,* *Pinus massoniana,* *Cunninghamia lanceolata*, etc.	*Cleistocalyx operculatus*, *Syzygium jambos*, *Castanopsis chinensis*, etc.
Height of EC (m)	40	39	27
Height of radiation and precipitation (m)	Above canopy 32 Below canopy 2 Precipitation 70	Above canopy 42 Below canopy 2 Precipitation 42	Above canopy 36 Below canopy 2 Precipitation 36
Profiles of air temperature and humidity (m)	2.5, 8.0, 22.0, 26.0, 32.0, 50.0, 61.8	1.6, 7.6, 11.6, 15.6, 23.6, 31.6, 39.6	4, 9, 15, 21, 27, 31, 36
Height of soil temperature and moisture (m)	Temperature 0.05 Moisture 0.05, 0.2, 0.5	Temperature 0.05 Moisture 0.05, 0.2, 0.5	Temperature 0.05 Moisture 0.05, 0.2, 0.5

[a] CBS, temperate deciduous broad-leaved and coniferous mixed forest which located on the northern slope of Changbai Mountain in northeastern China; QYZ, subtropical evergreen coniferous plantation which located at Qianyanzhou in eastern China; DHS, subtropical evergreen broad-leaved forest which located at Dinghu Mountain in southeastern China.

[b] Mean air temperature of 2003.

[c] Annual precipitation of 2003.

[d] The LAI at CBS was estimated during midseason.

recorded at 30 min intervals with a datalogger (CR10X & CR23X, Campbell Scientific Inc.). More extensive description of the instrumentations can also be found in Yu et al. (2006), Wen et al. (2006) and Guan et al. (2006).

2.3. Data processing

2.3.1. Flux calculation

A three-dimensional coordinate rotation was applied to the three-dimensional wind components, which aligned the horizontal velocity measurement normal to the mean wind streamlines and brought the mean lateral and vertical velocity components to zero. The effect of fluctuations in air density on the fluxes of CO_2 and H_2O was also corrected (Webb et al., 1980). Considering the CO_2 storage within the forest canopy, the net CO_2 exchange (N_{EE}) can be calculated as,

$$N_{EE} = \overline{w'\rho_c'} + \frac{m_a}{m_v}\frac{\overline{\rho_c}}{\overline{\rho_a}}\overline{w'\rho_v'} + \left(1 + \frac{m_a}{m_v}\frac{\overline{\rho_v}}{\overline{\rho_a}}\right)\frac{\overline{\rho_c}}{\overline{T}}\overline{w'T'} + F_s \tag{1}$$

where ρ_a, ρ_c and ρ_v are the density of dry air constitute, CO_2 constitute and water vapor constitute, respectively. m_a and m_v are the molecular mass of dry air and water, respectively. T is the temperature (K). The prime and overbar denote fluctuation and average, respectively. The first item in the right side of Eq. (1) is the net CO_2 flux measured by EC, the second item and third item represent the effect of fluctuations in air density on the measured CO_2 flux, and the last item, F_s is the CO_2 storage within the canopy. In this study, F_s was estimated as Hollinger et al. (1994),

$$F_s = \frac{\Delta c}{\Delta t} z_r \tag{2}$$

where Δc is the difference of CO_2 concentration between two adjacent levels, Δt is the time interval between the two adjacent measurements, and z_r is the measurement height. Δt is 1800 s in this study. In the following sections, N_{EE} away from the ecosystem to the atmosphere is positive.

2.3.2. Data filtering

To analyze the seasonal pattern of ecosystem photosynthetic capacity, only the daytime CO_2 flux data (Global radiation $>1\ W\ m^{-2}$) was selected in this study. The apparent abnormal data ($|N_{EE}| > 3.0$ mg $CO_2\ m^{-2}\ s^{-1}$) was removed from the analysis to reduce the uncertainty in subsequent analysis. The measurements during precipitation and extremely cloudy condition were also removed. After data filtering, 90%, 90% and 80.4% of daytime records were retained for CBS, QYZ and DHS site, respectively.

2.3.3. Estimation of ecosystem photosynthetic parameters

The daytime CO_2 fluxes were pooled into 5-day intervals and meteorological data were averaged or summed within the same period. Ecosystem α, $P_{\max}$ and R_e for each interval were estimated using the Michaelis–Menten equation (Falge et al., 2001),

$$N_{EE} = \frac{\alpha Q_{PPFD} P_{\max}}{\alpha Q_{PPFD} + P_{\max}} - R_e \tag{3}$$

where α (mg CO_2 μmol photon^{-1}) is ecosystem apparent quantum yield, $P_{\max}$ (mg CO_2 m^{-2} s^{-1}) the ecosystem maximum photosynthetic capacity, and R_e (mg CO_2 m^{-2} s^{-1}) is the daytime ecosystem respiration. Q_{PPFD} is the incident photosynthetic photon flux density (μmol photon m^{-2} s^{-1}).

2.3.4. Leaf area index (LAI)

The canopy LAI of CBS is estimated from the Q_{PPFD} measured above and within the canopy with Eq. (4) following Soegaard and Thorgeirsson (1998),

$$\mathrm{LAI} = -\frac{1}{k} \ln\left(\frac{Q_{PPFD,above}}{Q_{PPFD,below}}\right) \sin\theta \tag{4}$$

where $Q_{PPFD,above}$ and $Q_{PPFD,below}$ are the Q_{PPFD} measured above and below the canopy, respectively, θ the solar elevation angle, and k is the extinction coefficient of canopy. According to the field measurement, k was 0.55 at CBS. Both QYZ and DHS are evergreen forest, with the LAI of 3.6 and 4.0 m^2 m^{-2}, respectively.

3. Results

The seasonal patterns of ecosystem α, $P_{\max}$ and R_e of three different forest ecosystems estimated from Eq. (3) are plotted in Fig. 1. Figs. 2 and 3 show the seasonal variations of meteorological factors and LAI, respectively.

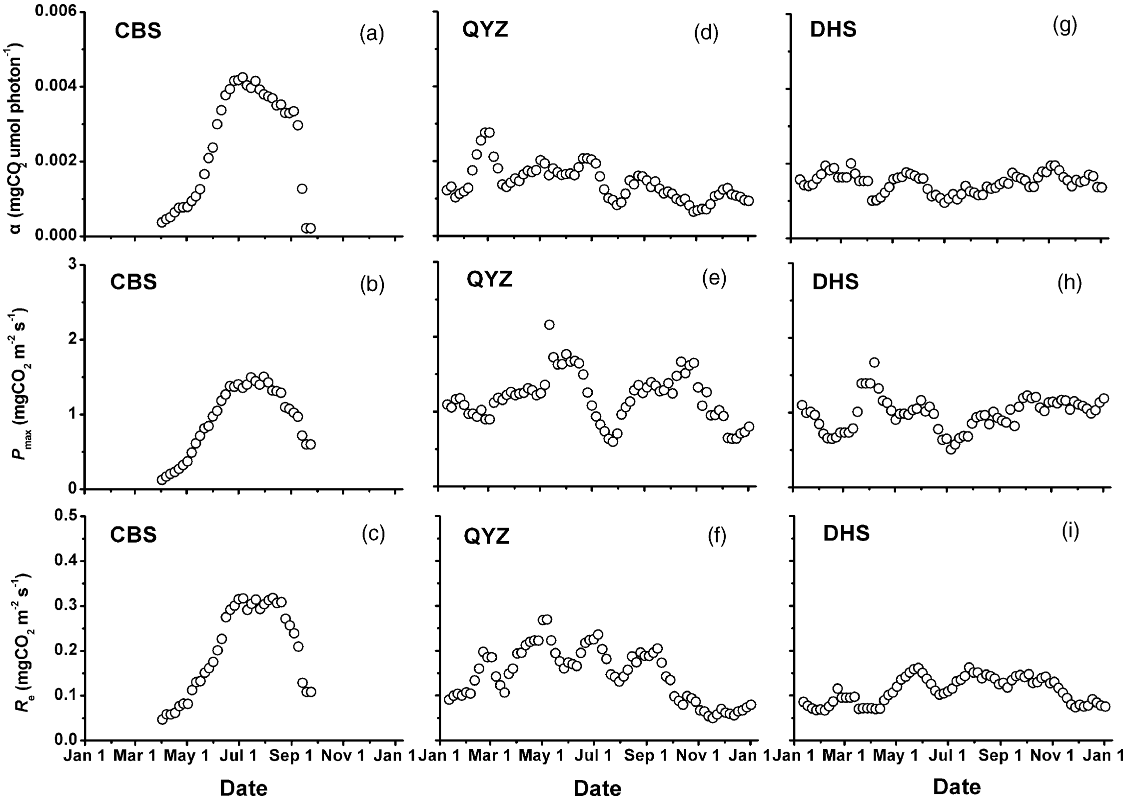

Fig. 1. Seasonal variations of ecosystem α, $P_{\max}$ and R_e of temperate mixed forest (CBS) (a–c), subtropical evergreen coniferous plantation (QYZ) (d–f) and subtropical evergreen broad-leaved forest (DHS) (g–i) in 2003. The parameters are derived from every 5 days with Michaelis–Menten model (Eq. (3)). In order to remove unnecessary noise, a running-mean filter with five windows is applied.

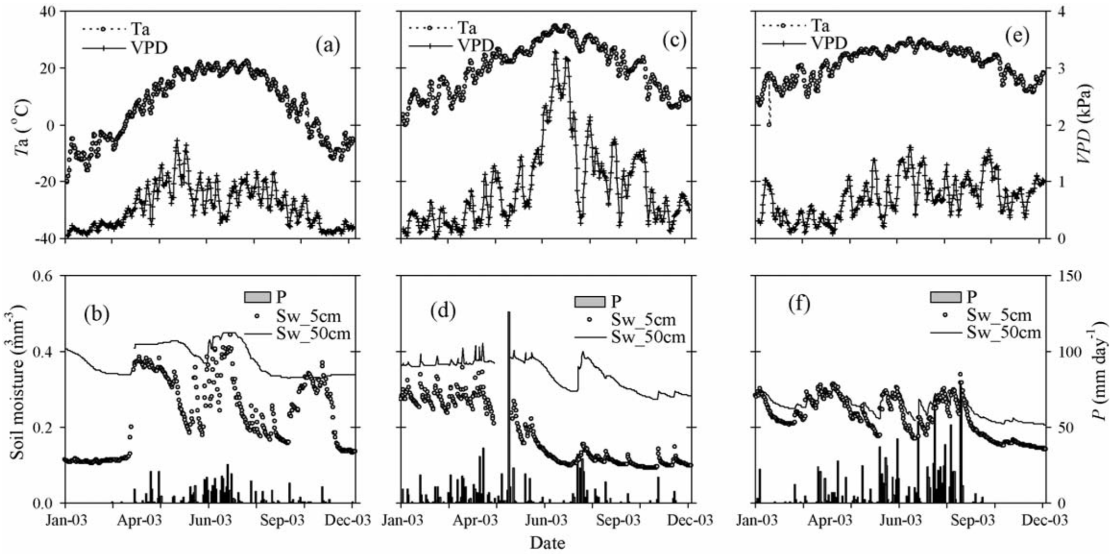

Fig. 2. The seasonal patterns of average daytime temperature and VPD (upper), soil water content and daily precipitation (bottom) of temperate mixed forest (CBS) (a and b), subtropical evergreen coniferous plantation (QYZ) (c and d) and subtropical evergreen broad-leaved forest (DHS) (e and f) in 2003. T_a is the air temperature; $S_{w\_5\ cm}$ and $S_{w\_50\ cm}$ are soil water content of 5 and 50 cm depth, respectively. A similar running-mean filter with five windows is also applied to the temperature and VPD to reduce the unnecessary noise.

3.1. Seasonal variations of ecosystem α

Figs. 1a, 2a and 3 show that the bell-shaped seasonal trend of ecosystem α coincided with the seasonal patterns of temperature and canopy development during the growing season of 2003 at CBS, which lasted from late March to early October. It increased from 0.0004 mg CO_2 μmol photon^{-1} in early April to the maximum of 0.0042 mg CO_2 μmol photon^{-1} in June, during which the LAI changed from 1.4 to 4.5 m^2 m^{-2} and temperature from 5 to 20 °C. However, ecosystem α decreased pronouncedly with the decrease in temperature and LAI in September, with the higher decreasing rate than the increasing rate in early spring.

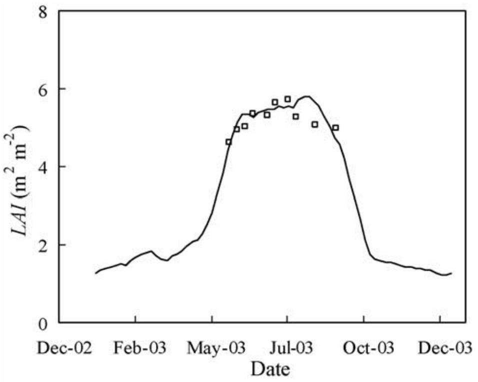

Fig. 3. The seasonal variation of leaf area index (LAI) of temperate mixed forest (CBS) in 2003. The solid line is the estimation from Eq. (4), and the dot is the measurement with LI-2000 (Li-Cor Inc., Lincoln, NE, USA).

At the CBS site, the analysis shows that the ecosystem α was mainly controlled by the temperature (Fig. 4a), which could be described with Arrhenus equation (Eq. (5)). Eq. (5) implied that ecosystem α could reach 0.0089 mg CO_2 μmol photon^{-1} while the temperature got to 25 °C if there was no other limitations.

$$\alpha = 0.0089\,e^{[15{,}406((1/298.16)-(1/(T+273.16)))]},\quad R^2 = 0.84,\quad n = 10 \tag{5}$$

In contrast, the seasonal pattern of ecosystem α at QYZ is not as apparent as that of CBS (Fig. 1d). Due to the influence of subtropical monsoon climate, the mean daytime air temperature was nearly 40 °C during the drought period, and the highest temperature exceeded 43 °C (data not shown). In the drought-stressed ecosystem, the vapor pressure deficit (VPD) increased to more than 3.0 kPa, while the soil moisture declined to around 0.1 m^3 m^{-3}. As a result of summer drought the ecosystem α declined apparently in late July.

At the QYZ site, it is obvious that ecosystem α decreases with the increasing VPD (Fig. 5a), and the potential maximum α was 0.0016 mg CO_2 μmol

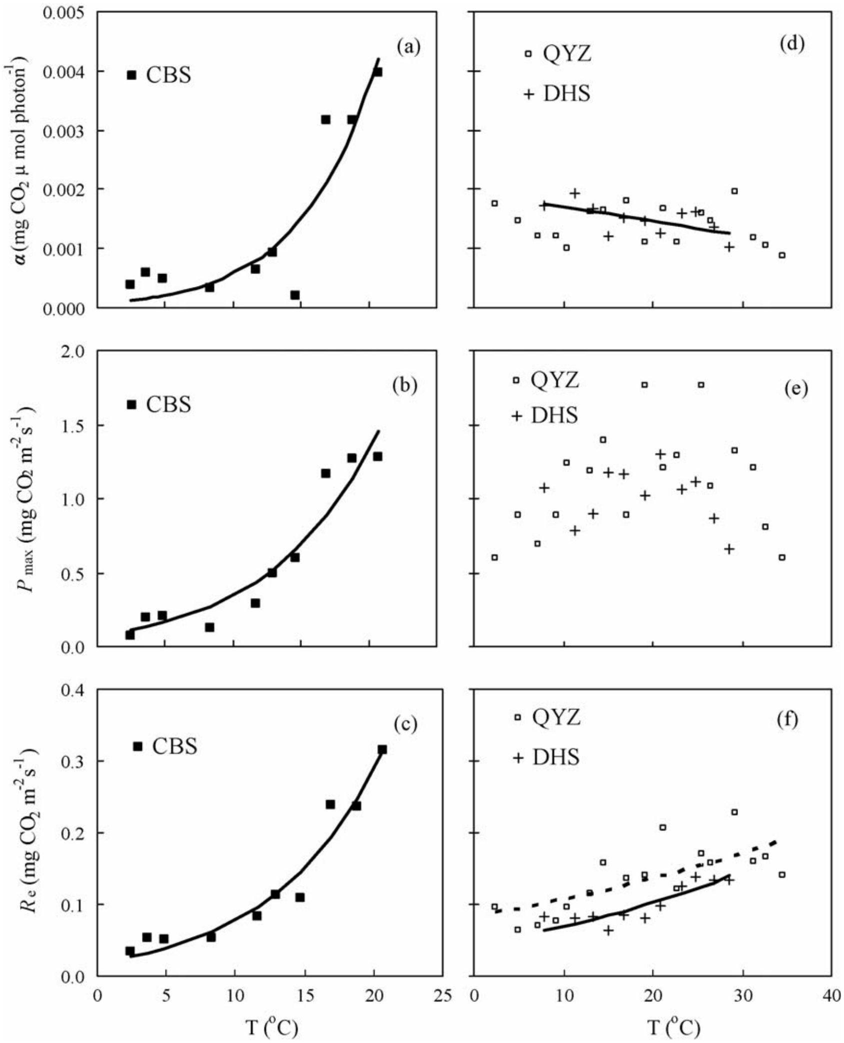

Fig. 4. The relationships between photosynthetic parameters (α, $P_{\max}$ and R_e) and air temperature at temperate mixed forest (CBS), subtropical evergreen coniferous plantation (QYZ) and subtropical evergreen broad-leaved forest (DHS). Each dot indicates the mean for 2 °C class.

photon^{-1} when there was no limitation of VPD (Eq. (6)).

$$\alpha = 0.0016(1 - 0.15\,\mathrm{VPD}), \quad R^2 = 0.44, \quad n = 15 \tag{6}$$

Ecosystem α at DHS also decreases during the summer which resulted from the similar influence of the drought stress as that of QYZ (Fig. 1g), while the magnitude and duration of the drought are less than at QYZ due to better water condition from plentiful rainfall (Fig. 2f). According to the statistic analysis, there exists significant negative correlation between ecosystem α and temperature (Fig. 4d). The temperature dependence of ecosystem α could be described by Eq. (7).

$$\alpha = 0.0020(1 - 0.012T), \quad R^2 = 0.39, \quad n = 11 \tag{7}$$

3.2. Seasonal variations of ecosystem P_{max}

Fig. 1b shows that ecosystem $P_{\max}$ of CBS had a similar seasonal pattern as that of ecosystem α (Fig. 1a). Partial correlation analysis showed that temperature was the dominant factor on the seasonal variation of ecosystem $P_{\max}$, and the relationship could be described by the Arrenhius function (Fig. 4b, Eq. (8)).

$$P_{\max} = 2.52\,\mathrm{e}^{[11{,}206((1/298.16)-(1/(T+273.16)))]}, \quad R^2 = 0.92, \quad n = 10 \tag{8}$$

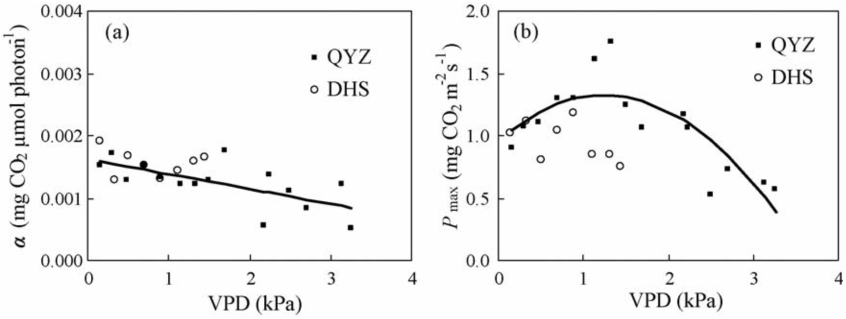

Fig. 5. The relationships between ecosystem α and $P_{\max}$ and water vapor deficit (VPD) in subtropical evergreen coniferous plantation (QYZ) and subtropical evergreen broad-leaved forest (DHS). Each dot indicates the mean for 0.3 kPa class.

As for the QYZ site, Fig. 1e shows that ecosystem $P_{\max}$ also declined apparently during the summer drought as that of ecosystem α (Fig. 1d), and it decreased nearly 50% during drought-stressed period.

Because of the high autocorrelation between temperature and VPD, it was very difficult to deconvolute whether the decrease in ecosystem $P_{\max}$ during the drought period was due to high atmospheric evaporative demand or to heat stress. A simple approach was attempted in this study to determine which factor was more important. Fig. 6 shows the relationship between the residuals of the N_{EE}–Q_{PPFD} regression and temperature or VPD. It is clearly seen that the residuals strongly depended on air temperature above 30 °C (Fig. 6b), as well as on VPD above 1 kPa (Fig. 6c). Statistical analysis shows that there exited significant correlation between the ecosystem $P_{\max}$ and VPD (Fig. 5b), and the ecosystem $P_{\max}$ could be estimated with Eq. (9), with a optimal value of 1.33 mg CO_2 m^{-2} s^{-1} when the VPD was 1.26 kPa.

$$P_{\max} = 1.33\left[1 - \frac{1}{2}\left(\frac{V_{\mathrm{PD}} - 1.26}{1.68}\right)^2\right],$$
$$R^2 = 0.66, \quad n = 15 \qquad (9)$$

Compared to the QYZ site, ecosystem $P_{\max}$ at DHS also decreases due to the influence of subtropical monsoon climate and attains the lowest, 0.51 mg CO_2 m^{-2} s^{-1}, in early July (Fig. 1h). However, there is no significant correlation with either temperature or VPD (Figs. 4e and 5b).

3.3. Seasonal variations of ecosystem R_e

Seasonal variation of ecosystem R_e was similar to that of to the temperature across the three forest ecosystems (Fig. 1c, f and i), which indicats the dependence of ecosystem respiration on temperature (Fig. 4f). During the midseason at CBS, the ecosystem R_e is much greater

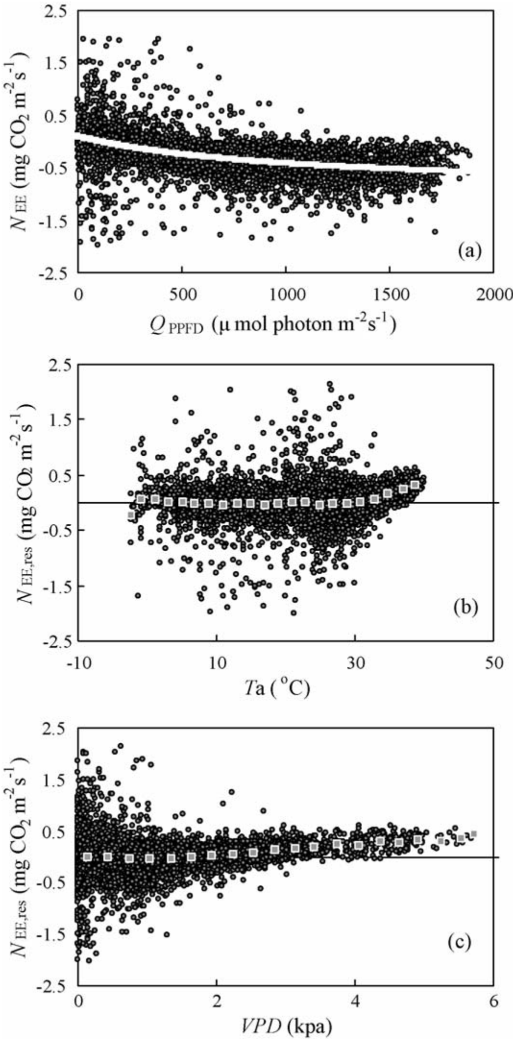

Fig. 6. (a) Relationship between N_{EE} and Q_{PPFD} for full daytime data of 2003 of subtropical evergreen coniferous plantation (QYZ). The solid line represents the non-linear regression of the Michaelis–Menten model (Eq. (3)). (b) Residuals of the data and the regression curve in panel (a) ($N_{\mathrm{EE,res}}$) vs. air temperature; squares indicate mean for each 2 °C, and (c) $N_{\mathrm{EE,res}}$ vs. VPD; squares indicate mean for each 0.3 kPa.

Table 2
Ecosystem photosynthetic parameters of different forest ecosystems

Forest	Period	α	P_{max} (μmol m^{-2} s^{-1})	R_e (μmol m^{-2} s^{-1})	Radiation[a]	Reference
Mixed forest	July–August 1995–1997	0.054 ± 0.005	37.9 ± 3.1	6.7±0.7	Q_o	Lee et al. (1999)
Harvard forest	September 1981	0.044	16.3	4.88	Q_o	Wofsy et al. (1993)[b]
Howland forest	1996	0.042 ± 0.02	17.4 ± 9.1	2.3 ± 1.7	Q_o	Hollinger et al. (1999)
	June–August	0.059 ± 0.008	23.6 ± 3.3	3.8 ± 0.4	Q_o	
Borea black spruce forest	June–August 2001	0.087 ± 0.006	38.1 ± 6.7	7.6 ± 2.0	Q_a	Griffis et al. (2003)
Boreal aspen forest	June–August 2001	0.067 ± 0.0058	16.7 ± 4.4	5.7 ± 1.9	Q_a	Griffis et al. (2003)
Boreal Jack pine forest	June–August 2001	0.040 ± 0.01	13.1 ± 4.7	3.4 ± 1.5	Q_a	Griffis et al. (2003)
Boreal aspen forest	1994, 1996	0.049 ± 0.005	18.6 ± 3.0		Q_a	Chen et al. (1999)
Scots pine	1999–2002	0.027 ± 0.006	14.5 ± 5.1	–	Q_o	Zha et al. (2004)
	June–September	0.027 ± 0.003	17.0 ± 3.7	–	Q_o	
Mixed forest	1997–2002	0.052 ± 0.020	11.5 ± 5.0	3.3 ± 0.8	S_g	Carrara et al. (2004)
	June–September	0.075 ± 0.007	17.1 ± 1.0	4.3 ± 0.2	S_g	
Mixed oak	July–August 1984	0.033	24.54	0.55	Q_o	Baldocchi et al. (1987)[b]
Macchia forest	November 1989	0.015	26.07	0.93	Q_o	Valentini et al. (2000)[b]
Mixed oak forest	August	0.033	15.32	3.94	S_g	Verma et al. (1986)[b]
Evergreen beech forest	July 1989–Marrch 1990	0.031 ± 0.039	8.8 ± 5.5	3.5 ± 2.7	Q_o	Hollinger et al. (1994)
	September–March	0.039 ± 0.007	10.5 ± 5.3	3.9 ± 3.1	Q_o	
Maritime pine forest	1991–1992	0.018	18.48	1.06	Q_o	Brunet et al. (1992)[b]
Tropical forest	1998–2000[c]	0.034 ± 0.018	29.7 ± 3.1	5.4 ± 0.8	Q_o	Loescher et al. (2003)
	1998–2000[d]	0.043 ± 0.013	45.0 ± 6.8	6.0 ± 1.7	Q_o	
	1998–2000[e]	0.036 ± 0.004	36.8 ± 4.0	5.9 ± 0.6	Q_o	
Tropical forest	Wet	0.07	29	1.2	Q_o	Vourlitis et al. (2003)
	Wet-dry	0.07	32.6	1	Q_o	
	Dry	0.07	11.7	0.3	Q_o	
	Dry-wet	0.07	20.7	0.9	Q_o	
	August 1999–July 2001	0.07	23.5 ± 9.3	0.9 ± 0.4	Q_o	
Rainforest	April–May 1987	0.049	18.31	11.11	S_g	Fan et al. (1990)[b]
CBS	2001	0.055 ± 0.036	20.6 ± 11.9	4.5 ± 2.6	Q_o	
	June–August	0.085 ± 0.015	29.8 ± 6.0	6.5 ± 1.5	Q_o	
QYZ	2001	0.032 ± 0.015	26.4 ± 11.0	3.2 ± 1.6	Q_o	
DHS	2001	0.034 ± 0.011	22.6 ± 8.5	2.5 ± 0.9	Q_o	

[a] The type of radiation used in Eq. (3), Q_o, incident photosynthetic flux density, Q_a, absorbed photosynthetic flux density, S_g, global radiation.

[b] The references are cited from Ruimy et al. (1995).

[c] $0 < \mathrm{VPD} < 0.5$ kPa.

[d] $0.5 < \mathrm{VPD} < 1.0$ kPa.

[e] $1.0 < \mathrm{VPD} < 1.5$ kPa.

than those of QYZ and DHS (Table 2). Meanwhile, the dependence of R_e on temperature was also described well by the Arrhenius equation (Eqs. (10)–(12)).

$$\mathrm{CBS}: \quad R_e = 0.54\,\mathrm{e}^{[10899.8((1/298.16)-(1/(T+273.16)))]}, \quad R^2 = 0.92, \quad n = 10 \tag{10}$$

$$\mathrm{QYZ}: \quad R_e = 0.15\,\mathrm{e}^{[1998.5((1/298.16)-(1/(T+273.16)))]} \quad R^2 = 0.53, \quad n = 17 \tag{11}$$

$$\mathrm{DHS}: \quad R_e = 0.12\,\mathrm{e}^{[3220.3((1/298.16)-(1/(T+273.16)))]}, \quad R^2 = 0.78, \quad n = 11 \tag{12}$$

4. Discussion

4.1. Effects of phenology on ecosystem α and P_{max} of CBS

For temperate and boreal forest ecosystems, the growth season and photosynthetic capacity were usually restricted by temperature and phenology (Falge et al., 2002a, b; Griffis et al., 2003). The development of LAI was an important aspect of phenology in such ecosystems. Temperature served as an indirect and dominant factor on ecosystem photosynthesis via its influence on the activity of photosynthetic system (Leuning, 1998) and on the amount of leaf area present.

For the temperate mixed forest (CBS), there was no apparent drought occurred in 2003 (Ren et al., 2005). It is shown that both the ecosystem α and $P_{\max}$ increase with temperature and LAI (Figs. 1–3), which implied that the photosynthetic activity of evergreen plants recovers quickly, with the activation of buds and leaf expansion when growing degree–days exceed the necessary minimum. The rapid increase of leaf photosynthetic area might act as the more important role in the efficient utilization of resource under the condition of limited radiation and temperature during the growing season.

In order to distinguish the respective effects of temperature and LAI on ecosystem photosynthesis, a simple approach was applied. Firstly, the ecosystem α and $P_{\max}$ were normalized by the corresponding LAI, and then multiplied by $\mathrm{LAI_b}$ (1.5 $\mathrm{m^2\ m^{-2}}$), which was the canopy LAI during the non-growth season and was assumed as the background LAI ($\mathrm{LAI_b}$) (Fig. 3). Thus we derived the ecosystem photosynthetic parameters α_T and $P_{\max,T}$, which denoted the effects of temperature on ecosystem photosynthesis with a background LAI (Fig. 7). The difference between α and α_T (or $P_{\max}$ and $P_{\max,T}$) represented the contribution of increased LAI from leaf expansion to ecosystem photosynthesis during the growth season. Fig. 7 also indicates that LAI might impose a more important effect on ecosystem photosynthetic capacity than temperature, which could also partly account for the increased annual accumulated N_{EE} under climate change with a warmer spring that resulted in early canopy development (Falge et al., 2002b).

4.2. Ecosystem α and P_{max}

Table 2 lists the photosynthetic parameters derived from different forest ecosystems. It shows there are great variations in the magnitude of ecosystem α, $P_{\max}$ and R_{e} among different forest ecosystems and seasons. The magnitude of photosynthetic capacity of CBS was within the varying range of temperate and boreal forest, while the ecosystem α and $P_{\max}$ of the coniferous forest (QYZ) were higher than that of boreal Scots pine forest (Zha et al., 2004), Jack pine forest (Griffis et al., 2003) and a Maritime pine forest (Brunet et al., 1992). The ecosystem α and $P_{\max}$ of subtropical evergreen broad-leaved forest (DHS) were higher than that of the evergreen beech forest (Hollinger et al., 1994) and rainforest (Fan et al., 1990), but they were still lower than that of the tropical forest (Loescher et al., 2003; Vourlitis et al., 2003).

During the growing midseason in 2003, the ecosystem α and $P_{\max}$ at CBS were higher than that of QYZ and DHS, while both QYZ and DHS are evergreen forest (Table 2). The probably reasons might be related to (1) the photosynthetic capacity of forest ecosystems with limited growing season usually was higher than forests that carried multiple years of foliage (Falge et al., 2002b), (2) the influence of severe drought on QYZ and the lower photosynthetic capacity of coniferous forest compared to broad-leaved forest (Griffis et al., 2003), and (3) the excessive rainfall and frequent fog events at DHS, which were not favor to ecosystem photosynthesis, especially the fog. From April to September, the mean cumulative daytime Q_{PPFD} were 31.18, 25.77 and 25.0 $\mathrm{mol\ m^{-2}\ d^{-1}}$ for CBS, QYZ and DHS, respectively, so the adaptive changes in photosynthetic capacity of DHS might occur under the long-term induction of low radiation. But more work was needed to test this assumption.

Table 2 also shows that the magnitude and sensitivity to temperature of ecosystem R_{e} at CBS was greater than at QYZ and DHS during the midseason. The ecosystem R_{e} were 0.54, 0.15 and 0.12 $\mathrm{mg\ CO_2\ m^{-2}\ s^{-1}}$ with a

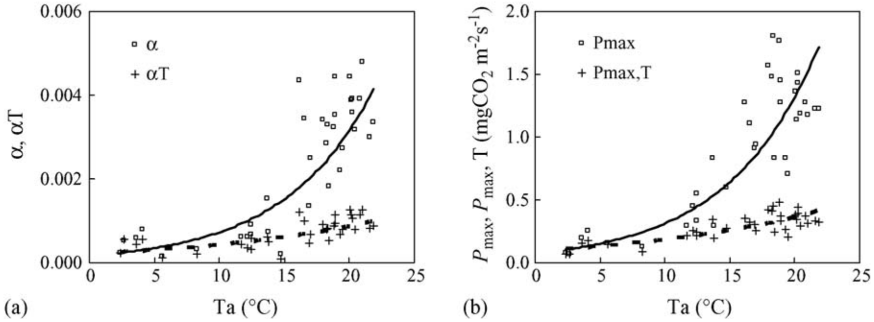

Fig. 7. Relative contribution of temperature (circle) to full ecosystem α (a) and $P_{\max}$ (b) of temperate mixed forest (CBS). The square indicates the ecosystem α and $P_{\max}$ derived from Michaelis–Menten model (Eq. (3)). The cross indicates the contribution to ecosystem α and $P_{\max}$ from temperature (α_T and $P_{\max,T}$) which is calculated as the product of background LAI ($\mathrm{LAI_b}$, 1.5 $\mathrm{m^2\ m^{-2}}$) and ecosystem α or $P_{\max}$ normalized with LAI. The solid and dash line indicate the exponential trendlines.

reference temperature of 25 °C at CBS, QYZ and DHS, respectively (Eqs. (10)–(12)). The probable reasons could be explained from two aspects. Firstly, the age of CBS was more than 300 years (Guan et al., 2006), so that the soil carbon content might be high and was liable to release more CO_2. Secondly, the high respiration rate coincided to the stronger photosynthetic capacity during the midseason (Reichstein et al., 2002). Therefore the response ecosystem R_e at CBS to the changing climate would be important in evaluating the ecosystem N_{EE}.

4.3. Effects of drought on ecosystem α and P_{max} of QYZ

The synchronization of high temperature and low moisture, which resulted from the subtropical monsoon climate, is the main climatic characteristics during summer at the QYZ site. During the summer of 2003, a severe drought occurred which marked with extremely high temperature, high VPD and the low soil water content (Fig. 2c and d), and the ecosystem α and P_{max} declined significantly (Fig. 1d and e).

Ecosystem photosynthesis was largely dependent on leaf area, radiation, air temperature, VPD and available soil water (Baldocchi, 1997; Tuzet et al., 2003). The reduction of photosynthesis under dry conditions could be addressed by the theory of ‘classical stomatal control’ and ‘non-stomatal control’. Many studies indicated that the reduction of photosynthesis was related to the variation of stomatal conductance with water stress (Baldocchi, 1997; Anthoni et al., 2002). Farquhar and Sharkey (1982) indicated that high VPD would strongly limit plant photosynthesis by stomatal closure. At the QYZ site, both temperature and VPD exerted great effect on ecosystem photosynthesis, of which VPD could be a more restrictive factor than temperature during the severe drought (Fig. 6). However, Reichstein et al. (2002) hypothesized that the decrease of photosynthesis of Mediterranean evergreen forest during drought period also resulted from the reduction of mesophyll photosynthetic activity and mesophyll conductance, stomatal patchiness and photoinhibition, which were assumed as ‘non-stomatal control’. Compared with the Mediterranean evergreen forest (Reichstein et al., 2002), the drought stress was more severe at QYZ. The above analysis implied that the decrease of photosynthesis at QYZ during the drought period might be the combined influence of stomatal control and non-stomatal control. However, the underlying mechanism of the impact of drought on the N_{EE} needed to be further studied.

Fig. 5b shows that the P_{max} of QYZ reached a maximum with a moderate VPD around 1.26 kPa. This is similar to the result of Loescher et al. (2003) that also shows a maximum photosynthetic rate when VPD >0.5 kPa, and Vourlitis et al. (2003) also indicates that the optimal ecosystem P_{max} in the wet season is lower than that of wet-dry transition season in a tropical forest ecosystem (Table 2). It could be explained by lower VPD representing lower temperature and/or higher humidity, neither of which is favorable to ecosystem photosynthesis. While excessively high VPD would also limit the ecosystem photosynthesis usually due to high atmospheric demand with water limitation. Therefore, ecosystem shows a maximum photosynthesis at certain VPD (Fig. 5b).

5. Conclusions

Seasonal patterns and the environmental responses of α and P_{max} in three typical forest ecosystems along the North–South Transect of Eastern China (NSTEC) were investigated. The seasonal variations of ecosystem α and P_{max} at CBS were mainly determined by the temperature and phenology. The effect of temperature on ecosystem photosynthesis derived from its influence on the activity of photosynthetic system and on the amount of leaf area. The phenology in such a temperate forest, which was mainly embodied by the development of LAI, also played great influence on ecosystem photosynthesis. The ecosystem photosynthetic capacity of QYZ was mainly influenced by drought which resulted from the subtropical monsoon climate in 2003, both ecosystem α and P_{max} at QYZ showed negative correlation with VPD significantly. It was presumed that both the stomatal control and non-stomatal were responsible for the decrease of ecosystem α and P_{max}. The effect of the drought on DHS was not so apparently as that on QYZ due to the abundant rainfall and mild temperature. Compared to CBS and QYZ, there was not a dominant factor responsible for the seasonal fluctuation of ecosystem P_{max} at DHS, while there was only weak negative correlation between α and temperature.

During the growing midseason in 2003, the ecosystem α and P_{max} at CBS were higher than that of QYZ and DHS. The probably reasons might be related to differences of the inherent photosynthetic capacity between short lived foliage and multiple-year foliage and the influence of environmental conditions which including the severe drought at QYZ and the excessive rainfall and frequent fog events at DHS, however the validation of such hypothesis was necessary in the future study. The ecosystem respiration of the three forest ecosystems exhibited significant correlation with temperature, and the magnitude and sensitivity to temperature of ecosystem R_e at CBS was greater than of QYZ and DHS during midseason. It was hypothesized that the old age (>300 year) and higher photosynthetic capacity were responsible for the stronger R_e, so the response of R_e at CBS to changing climate and influence on the carbon budget of such ecosystem deserved more attention.

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